THE BIOLOGICAL CONTROL OF THE WEED *ACACIA LONGIFOLIA* BY THE GALL WASP *TRICHILOGASTER ACACIAELONGIFOLIAE:* A STUDY OF A PLANT-INSECT INTERACTION

by

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PREFACE

"Weeds are responsible for about 30 percent of all crop losses worldwide, but all weed research, including biological control, receives only about 10% of crop pest control support. The impact of weeds is insidious, diffuse, and complex Increased use of biological control may help to reduce the massive quantity of energy and time now expended for weed control worldwide." Batra (1981)

"The vitality of biocontrol of weeds requires two types of evaluation before a project is completed. To maintain financial support it is necessary to show that biocontrol is an economical method of solving certain types of weed problems and to improve the effectiveness of biocontrol in the future, it is necessary to have scientific feed-back. Essentially, the first type of evaluation is concerned with what has been achieved and the second with why the result, either success or failure, has been achieved." Harris (1980a)

The biological control of weeds using insects is a young science. The first intentional use of an insect to control a weed was in 1863 in India where the cochineal insect, *Dactylopius ceylonicus* (Green), was dispersed to control *Opuntia vulgaris* Miller some 68 years after the accidental introduction of this insect to that country (Goeden, 1978; Moran & Zimmermann, 1984). However, the first full scale attempt at a classical weed biocontrol programme was against *Lantana camara* L. in Hawaii in 1902 (Goeden, 1978; Harley, 1985a). By 1984 there had been 499 releases of exotic invertebrates and fungi, 488 of which were insects, for the control of 101 weed species in 70 countries (Julien *et al.,* 1984).

Despite this marked increase in the number of biocontrol programmes in later years, attempts which failed have rarely been studied or documented and even successes are seldom adequately quantified. This has been implied by Harley (1985a), Julien, (1982), Julien *et al.* (1984) and Maw (1984). The pressure to produce results and the difficulty of determining the reasons for failures are prohibitive (Dennill *et al.,* 1987; Appendix 6; Goeden & Louda, 1976). The advancement of this science thus relies heavily on the study of its successes.

This thesis is an evaluation of the gall wasp *Trichilogaster acaciaelongifoliae* as a biocontrol agent for the weed *Acacia longifolia* in South Africa. The wasp has been successful, and, in accordance with Harris (1980a), my aims were twofold: to quantify that success and to provide reasons for it. This information not only produces guidelines

for the future selection of biocontrol agents, *sensu* Harris (1980a), but also serves as a means of enhancing our understanding of insect-plant relationships.

In addition, this thesis provides an indication of the potential of gall forming insects in biological control of weeds. Gall formers have seldom been used to control weeds (Julien, 1982; Maw, 1984). Since their effects are indirect compared with those of insects attacking vegetative plant parts, their potential for weed biocontrol has apparently been underestimated in the past by some authors (Goeden, 1983; Harris, 1973; Hokkanen, 1985a). The present attempt is the first ever in which a gall forming hymenopteran has been used to control a weed, and shows beyond doubt that certain gall formers can have strong potential in this field.

Chapter 1 concerns the establishment of the wasp, its population increases, dispersal, host-seeking, and the reduction of reproductive potential of *A. longifolia* populations. The development of new techniques that were necessary for the determination of these parameters is included. Emphasis is placed on the reasons for the successful establishment and rapid population increases observed.

The potential of the insect for suppressing both reproduction and growth of the weed is great, and is examined in detail in Chapter 2. The phenological information obtained during the course of this study showed important inadequacies in the knowledge of the phenology of *A. longifolia.* This is rectified in Chapter 3 in which the implications of an incomplete understanding of weed phenology for biological control are emphasised. In particular, the resource allocation between reproduction and growth of the plant provides a crucial setting for the next chapter. In Chapter 4 the nature of the galling by *T. acaciaelongifoliae* and its relation to the phenology of *A. longifolia* are examined in order to explain how the wasp is able to exploit its host so effectively under South African conditions.

Chapter 5 deals with the release of the wasp throughout the South African range of the weed and the identification of regions in which its performance appears inadequate. The climates of South Africa and Australia are compared to determine to what degree the establishment of *T. acaciaelongifoliae* in various regions in South Africa is related to the climate of the regions in which the wasp was collected in Australia. This chapter includes maps illustrating weed distribution, co-ordinates for all release points, and documents the method whereby the wasps were released.

Chapter 6 is an essay dealing with the implications of the study, both practical and theoretical. Recommendations regarding the future selection of biocontrol agents *are* made, with emphasis on perspectives emerging from this thesis, and the future role of the wasp in the control of *A. longifolia* in South Africa is discussed.

CONTENTS

INTRODUCTION

The long-leafed wattle *Acacia longifolia* (Andr.)Willd. (Fabaceae), which grows as a tree or shrub, is indigenous to south-eastern Australia (Costermans, 1981). Of the Australian plants introduced to South Africa for dune binding during the early nineteenth century, A. *longifolia* was one of the least widely planted and least successful (Shaughnessy, 1980). However, it has subsequently become a major threat to river systems, catchments and conservation areas throughout the south-western, southern and south-eastern Cape Province (Boucher & Stirton, 1978; Macdonald *et al.*, 1985).

Although *A. longifolia* survives on drier mountain slopes, this plant grows best and is most invasive along riverbanks and in moist valleys and catchments (Boucher & Stirton, 1978) (Plate 1). Using a rating system based on the current area infested, potential habitat, potential rate of spread, ease of control and impact on the ecosystem, A. *longifolia* was recently rated the second most important invasive plant species in the highly endangered fynbos biome (the Cape Floristic Kingdom) (Macdonald & Jarman, 1984). Although there is debate regarding the relative importance of the factors contributing to the invasiveness of this weed (Macdonald, 1984), its high production of long-lived seeds (Plate 2) which accumulate in the soil in the abscence of predation or other destructive factors is undoubtedly paramount (Milton & Hall, 1981). Seed bank densities can reach 34000 seeds/m^2 (Pieterse, 1986) and these seeds are stimulated to germinate *en masse* by fire (Pieterse & Cairns, 1986) (Plate 1). Fire is a frequent and necessary feature in fynbos ecology (Kruger & Bigalke, 1984; Milton, 1980; van Wilgen, 1982). The spread of *A. longifolia* is further encouraged by the use of fire in the control of *Hakea sericea* Schrad. (Fenn, 1980), another major invasive Australian shrub (Annecke & Neser, 1977; Fugler, 1982).

The gall wasp *Trichilogaster acaciaelongifoliae* Froggatt (Pteromalidae) was introduced into South Africa to limit the invasiveness of A. *longifolia* by reducing its seed production (Dennill, 1985; Appendix 1; Neser, 1985; van den Berg, 1979). Another reason for the selection of the gall wasp, rather than an insect which attacks vegetative parts of the plant, was the conflict between conservationists on the one hand and the black wattle and black wood industrialists on the other. Black wattle *(Acacia mearnsii* De Wild.) is grown in Natal for chip board, pulp, tannins and timber. Profits accrued are estimated at 14 million rands *per annum (7* million US $) (A.P.G. Schonau, Research Scientist, Institute for Commercial Forestry Research, personal communication). Black wood *(Acacia melanoxylon* R.Br.) is grown in the southern Cape Province and used for

Plate 1

Top.	A typical riverine infestation of *A. longifolia* showing the profusion of yellow flowers which this weed bears during spring (September).
Middle.	A montane infestation of *A. longifolia* (left) threatening the indigenous forest (right) of a mountainous region in the southern Cape Province.
Bottom.	A mountainside covered with *A. longifolia* seedlings which germinated *en masse after a fire.*

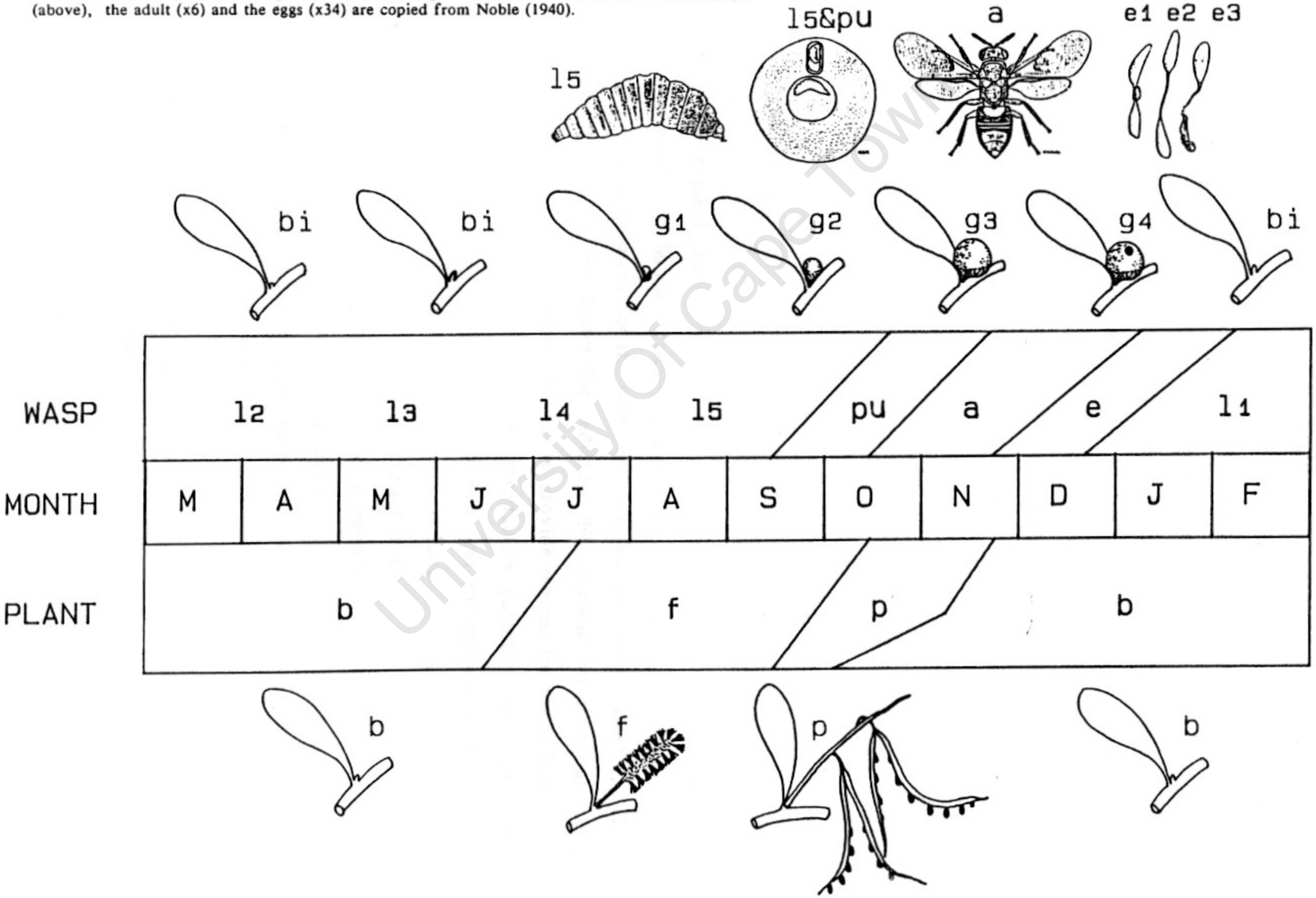
Plate 2

Top.	**Branches of *A. longifolia* heavily laden with ripe pods and seeds in mid-November.**
Left.	**An adult *T. acaciaelongifoliae* female ovipositing in an *A. longifolia* reproductive bud which is situated in the aril between the phyllode and the branch. The ovipositor (between the second and third legs) can be seen penetrating the bud.**
Right.	**A cross section of a three-chambered gall showing larvae (white) in the two chambers on the left and a pupa (black) in the chamber on the right. Courtesy Dr. S. Neser.**
Bottom.	***Acacia longifolia* trees bearing no pods as a result of heavy galling by *T. acaciaelongifoliae.* The branches also show die-back of the shoot tips and the loss of phyllodes attributed to the galling.**

furniture. The fear that biocontrol agents that attack vegetative parts of adult Australian acacias may be non-specific, and hence become pests on these commercial species, has resulted in a compromise which dictates that only insects which inhibit reproduction may be released (Neser & Moran, 1985). These fears are not unfounded, since a leaf feeding bug *Rayiera* sp. (family: Miridae), has already been rejected as an agent for A. *longifolia* because it also fed on *A. mearnsii* and *A. melanoxylon* (Donnelly, 1986). It is also generally maintained that insects which attack and live in the reproductive parts of their hosts display a higher degree of host specificity than do those attacking the *vegetative* parts of their hosts: this seems to be especially true of pre-dispersal seed attacking insects (Janzen, 1970, 1975, 1976, 1980), including seed attacking insects on Australian acacias (Auld, 1983) and gall forming insects (Mani, 1964, Ananthakrishnan, 1984).

Trichilogaster acaciaelongifoliae was proposed as a biocontrol agent for *A. longifolia* in South Africa by van den Berg (1979). Neser (1985) subsequently collected and exported the wasp from Australia to South Africa where it was released in 1982 and 1983 by myself and Mr J.A. Gordon (Dennill, 1985; Appendix 1). *Trichilogaster acaciaelongifoliae* is univoltine, but bivoltinism occurs rarely (van den Berg, 1979). The phenology of the wasp in relation to its host plant is illustrated in Fig. 1. The galls develop during spring when *A. longifolia* flowers. Adult wasps, which are on average three millimeters in length, emerge from late October to January, but mainly in November when the pods ripen. Adult females live for an average of 2.3 days, are parthenogenetic, highly fecund (mean of 409 eggs/female), and are able to begin ovipositing immediately (Noble, 1940). Eggs are laid in reproductive and vegetative buds which are destined to become inflorescences or branches during the next spring (Plate 2). Depending on the number of eggs laid in a bud and survival of eggs and larvae, the number of chambers (containing one insect each - see Plate 2) per gall varies from one to seven. Galls containing up to 24 *T. acaciaelongifoliae* are occasionally found. The galls develop in the axils of the phyllodes, are green throughout most of their development, and look like small beads (1-4 mm in diameter) which are either single or in clusters depending upon whether they are single or multi-chambered. The galls increase in size throughout their development and in November and December the mature galls change colour and look like clusters of reddish green marbles. At this stage the galls are visually most striking and can be seen from a distance, giving branches of heavily galled *A. longifolia* trees the appearance of strings of shiny beads (Plate 2). After adult emergence the galls desiccate, become shrivelled and turn brown as the gall tissue dies and become more difficult to see from a distance, especially as the trees put

Fig. 1. The annual life cycle of *T. acaciaelongifoliae* in relation to the reproductive phenology of *A. longifolia*. The sketches are drawn to correspond with the appropriate months of the year. b = reproductive bud, f = flower development, p = pod development, l = larva (l1, l2, l3, l4 & l5 = 5 larval instars), pu = pupa, a = adult, e = egg (e1 & e2 = ovarian eggs with connecting tube folded and extended, respectively, e3 = egg a few hours after oviposition), bi = infested bud within which the first four larval instars develop without any external signs of the bud being infested, g1 & g2 = gall developing instead of inflorescences, g3 = mature gall containing fifth larval instar and/or pupa, g4 = mature gall showing an emergence hole after being evacuated by an adult. The drawings (from left to right) of the fifth larval instar (x10), the cross section of a mature gall (x1.2) containing a last instar larva (center) and a pupa (above), the adult (x6) and the eggs (x34) are copied from Noble (1940).



on new growth. Whether one or more insects develop per gall, inflorescence development is always prevented.

The phenology of *A. longifolia* has been studied by Milton (1980). Vegetative growth of leader shoots and lateral branching occurs during the spring and the early summer months from September to December, and declines during late summer. A secondary growth flush occurs in autumn. The reproductive phenology of *A. longifolia* is illustrated in Fig. 1. The plant reproduces annually during spring. The inflorescences develop from July onwards. The flowers open in August and abscission of unfertilised inflorescences occurs in September. Pod filling occurs during late September, October and November. Pods ripen, dehisce and drop seeds in mid-November. *The reproductive buds from which inflorescences develop are produced during the spring growth flush of the preceding year.*

The growth habit of *A. longifolia* varies from shrub- to tree-like at various sites. On mountain slopes away from running water, A. *longifolia is* a shrub whereas along riverbanks the plants are less dense and become taller trees. *Acacia longifolia* also often occurs as a roadside weed, the result of dispersal of seeds with building sand and disturbance of the indigenous vegetation caused by roadbuilding (Macdonald & Richardson, 1986).

The aims of the present studies were (1) to determine whether the wasp would establish on *A. longifolia* in South Africa, and if so, to quantify the degree of establishment and to provide reasons for it, whether successful or poor (Chapter 1), (2) to determine the potential of this insect for reducing the reproductive potential and vegetative growth of *A. longifolia* (Chapter 2), (3) to provide reasons for the ability, or inability, of the wasp to reduce effectively the reproductive potential and vegetative growth of the weed (Chapters 3 & 4), (4) to release and extensively evaluate the establishment of the wasp throughout the South African range of the weed, and to provide reasons for the success or failure of establishment in the regions in which either occurred (Chapter 5), and (5) to determine how useful current theory would have been in predicting the outcome of this biocontrol attempt, and to evaluate this project critically in order to determine whether this thesis provides new insights into plant-insect relationships that may be of use in the future selection of biocontrol agents (Chapter 6).

With the exception of (4) above the studies were all intensive and were executed at six sites, the localities of which *are* mapped in Fig. 2 and the co-ordinates and site descriptions of which are given in Table 1. Each chapter consists of a number of separate studies with disparate methods. For ease of reading, the methods and results for each study are given together in a ‘Methods and Results’ section for each chapter. Unless stated otherwise, statistical methods and notations are those of Snedecor and Cochran (1967).

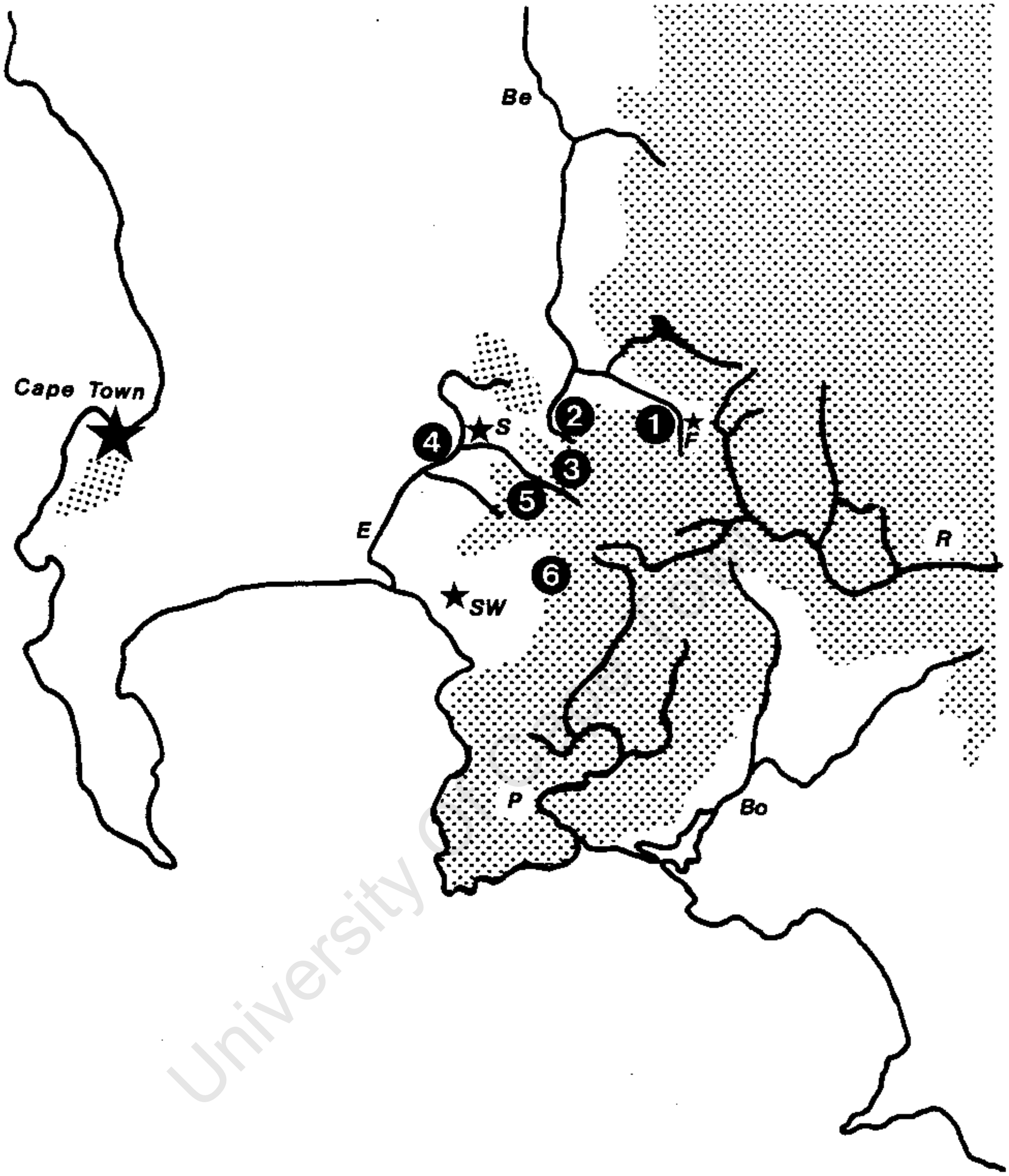


Fig. 2. The location of the six sites in the south-western Cape Province at which intensive studies were done on the establishment and the ability of the gall wasp ***T.** acaciaelongifoliae* to exploit its host plant *A. longifolia* under South African conditions. 1 = Franschhoek, 2 = Banhoek River, 3 = Banhoek Mountain, 4 = Eerste River, 5 = Stellenbosch Mountain, 6 = Vergelegen. The stars represent cities or towns: F = Franschhoek, S = Stellenbosch, SW = Somerset West. Be = Berg River system, E = Eerste River system, P = Palmiet River system, Bo = Bot River system and R = Riviersonderend river system. The shading represents mountainous regions with an elevation >1500 m.

TABLE 1 The co-ordinates, site descriptions and density of *A. longifolia* shrubs or trees for the six sites in the south-western Cape Province at which intensive studies were done on the establishment and the ability of the gall wasp *T. acaciaelongifoliae* to exploit its host plant *A. longifolia* under South African conditions. These sites are all situated in the south western Cape Province which has a mediterranean climate. Approximately 59% of the rain (1700mm/annum) falls during winter (May to August), and January is the warmest month (mean 22°C).

Site name and type	Co-ordinates	Tree or shrub density & height
Franschhoek (riverine)	19°7'E;33°54'S	<1 to 5 trees/$(10\text{-m})^2$ 2 to >10 m tall
Banhoek River (riverine)	18°58'E;33°56'S	"
Banhoek Mountain (montane scree)	18°58'E;33°56'S	1 to 20 shrubs/$(10\text{-m})^2$ 1 to 4 m tall
Eerste River (riverine)	18°51'E;33°56'S	"
Stellenbosch Mountain (moist kloof)	18°54'E;33°57'S	1 to 2 trees/$(1\text{-m})^2$ up to 8 m tall
Vergelegen (montane foothills)	18°56'E;34°3'S	"

CHAPTER 1

Establishment of the gall wasp *Trichilogaster acaciaelongifoliae* (Pteromalidae) as a biological control agent for the weed *Acacia longifolia* in South Africa

ABSTRACT

Trichilogaster acaciaelongifoliae Froggatt was introduced to South Africa to reduce seed production of the weed *Acacia longifolia* (Andr.)Willd. In this chapter, population increases and dispersal patterns and rates of the wasp are reported for two study sites. Populations of the wasp increased so dramatically that the third generation after release had galled 84% and 80% of the branches on trees at the two study sites, respectively. The wasps had dispersed throughout the 100- by 100-m study sites within two generations. The technique developed for monitoring population increases and pattern of dispersal of the wasp is based on determining the number of branches/tree and percentage of branches galled/tree using basal tree circumference and visual estimations of the percentage of galled branches/tree, respectively. This method is >90% quicker than counting galled branches and enables extensive monitoring of the agent. Salient features of the wasp which enhanced its establishment are examined. The parthenogenetic, highly fecund females outnumbered males by 5:1. Multiple gall formation is shown to contribute to high establishment rates because multiple galls produced more wasps/unit dry weight of gall tissue than did single galls, and constituted a high proportion (66%) of the galls. Parasitism of the gall wasp was negligible: if it occurred at all, the percentage co-emergence of Hymenoptera, some of which could have been parasitic, from galls at five sites over two years was 0.1 to 1.6%. The gall wasp is shown to be very efficient at locating and utilising reproductive buds on trees of different shapes and sizes. This excellent host seeking ability coupled with wind dispersal and directed flight has enabled establishment at sites 20 km from release points. All these abilities, in conjunction with the large wasp populations contributed significantly to the successful dispersal and establishment of this agent. After only three generations since release, the gall wasp had reduced seed production at the two study sites by between 73 and 91%, and 83 and 95%, respectively.

The aims of the studies reported in this chapter were (a) to monitor *T. acaciaelongifoliae* population increases, levels of infestation and seed reduction achieved in *A. longifolia* populations, (b) to examine the rate and pattern of dispersal of the wasp and its ability to locate and utilise its host and (c) to provide the reasons for the success or failure of establishment. The latter includes an examination of the effect of multiple gall production, sex ratios, incidence of parasitism and loss of galls between spring and midsummer, on population growth. This chapter is thus essentially an evaluation of features of the insect which either contribute to or hamper its establishment in its new environment. This information, which has been published by Dennill (1987 in press) (Appendix 2), is a pre-requisite to the following chapter in which the potential of the wasp for reducing seed production and vegetative growth of its host is examined in detail.

METHODS AND RESULTS

Population increases, increasing infestation levels and dispersal

At both Vergelegen and Banhoek a 100- x 100-m area was marked in an *A. longifolia* infestation. Tree density at the two sites ranged from 2 to 20 and 2 to 5 trees/(10-m)^2, respectively. Within the plots, *A. longifolia* trees were marked at 10-m intervals on 10 transects which were 10 m apart. The plots were located such that the points where the wasps were released were central. In December 1981, 217 and 48 female *T. acaciaelongifoliae* were caged in gauze sleeves on 21 and 10 branches of *A. longifolia* at Vergelegen and Banhoek respectively. The sleeves were removed after seven days when the females, which live for 2.3 days on average (Noble, 1940), had oviposited and died. During subsequent seasons, the wasps were allowed to disperse naturally. During spring 1982, the emergence holes on the galls produced by the caged females were counted, and during the next spring (1983) the number of emergence holes on the galls in the four 10- x 10-m quadrats around the release point were counted. Only the four central quadrats were counted since visual assessments indicated that at least 75% of the total population was located immediately around the release points. At Vergelegen, however, the number of galls in the four central quadrats was too high (42882) to count the exact number of emergence holes. The percentage emergence in a sample of 765 galls was 75.4%. This figure was used to estimate the number of wasps that emerged from the galls counted at Vergelegen in 1983.

The rapid increase of the *T. acaciaelongifoliae* populations after two years (Table 2) necessitated the development of a less time consuming method of estimating levels of infestation which could also be used to monitor rate and pattern of dispersal of the gall wasp and its effects in stands of *A. longifolia.*

A quick method of estimating the proportion of galled branches per tree was tested. A total of 43 trees of various sizes (ranging from 22 to 5616 branches/tree) and degree of infestation by the gall wasp were selected from Vergelegen, Banhoek and Eerste River. The percentage of galled branches per tree was estimated after viewing each tree from all sides. Thereafter the number of galled and ungalled branches on each tree were counted to calculate the actual percentages of galled branches.

TABLE 2 The number of *T. acaciaelongifoliae* adults that emerged from galls on *A. longifolia* at Vergelegen and Banhoek for two generations after release in 1981.

Site	Year	No. adults	Remarks
Vergelegen	1981	205	Released
	1982	2245	1st generation
	1983	>32333	2nd generation
Banhoek	1981	48	Released
	1982	235	1st generation
	1983	>1250	2nd generation

In order to determine whether basal tree trunk circumference could be used to estimate the number of branches per tree, tree trunk circumferences were measured (mm) at ground level and the number of branches per tree were counted for 23 and 4 trees at Vergelegen and Banhoek, respectively. The number of branches per tree ranged from 22 to 4145.

Visual estimations of the proportion of galled branches on a tree were accurate when compared with the actual proportions (Fig. 3) and basal tree trunk circumference is a reliable indicator of the number of branches per tree (Fig. 4). These relationships were used to determine (a) the number of galled branches on the marked trees on the plots at Vergelegen and Banhoek, (b) the total number of branches on marked trees and (c) the percentage of galled branches on each of the marked trees. The annual increase in the number of galled branches at the sites was used as an indicator of population increment. The total number of branches sampled at each site was determined to calculate annual increases in the percentage of branches galled by the wasp relative to the annual increments in number of branches. The percentage of galled branches on each tree was recorded separately to illustrate visually the increasing levels of infestation and the rate and pattern of dispersal of the wasp.

The gall wasp populations, monitored by estimating the number of galled branches on sampled trees, increased exponentially from 1982 to 1985 at Vergelegen and Banhoek (Fig. 5) (regression equation $y = a.e^{(bx)}$, $r^2 = 0.98$ & 0.99, respectively). The percentage of branches galled at both sites also increased similarly, culminating in 84% and 80% of the branches on the Vergelegen and Banhoek plots being galled in 1985 (Figs. 5A & B).

In 1983 the highest concentrations of galls were around the release points with light infestations scattered around them (Fig. 6). This pattern changed in 1984 when the

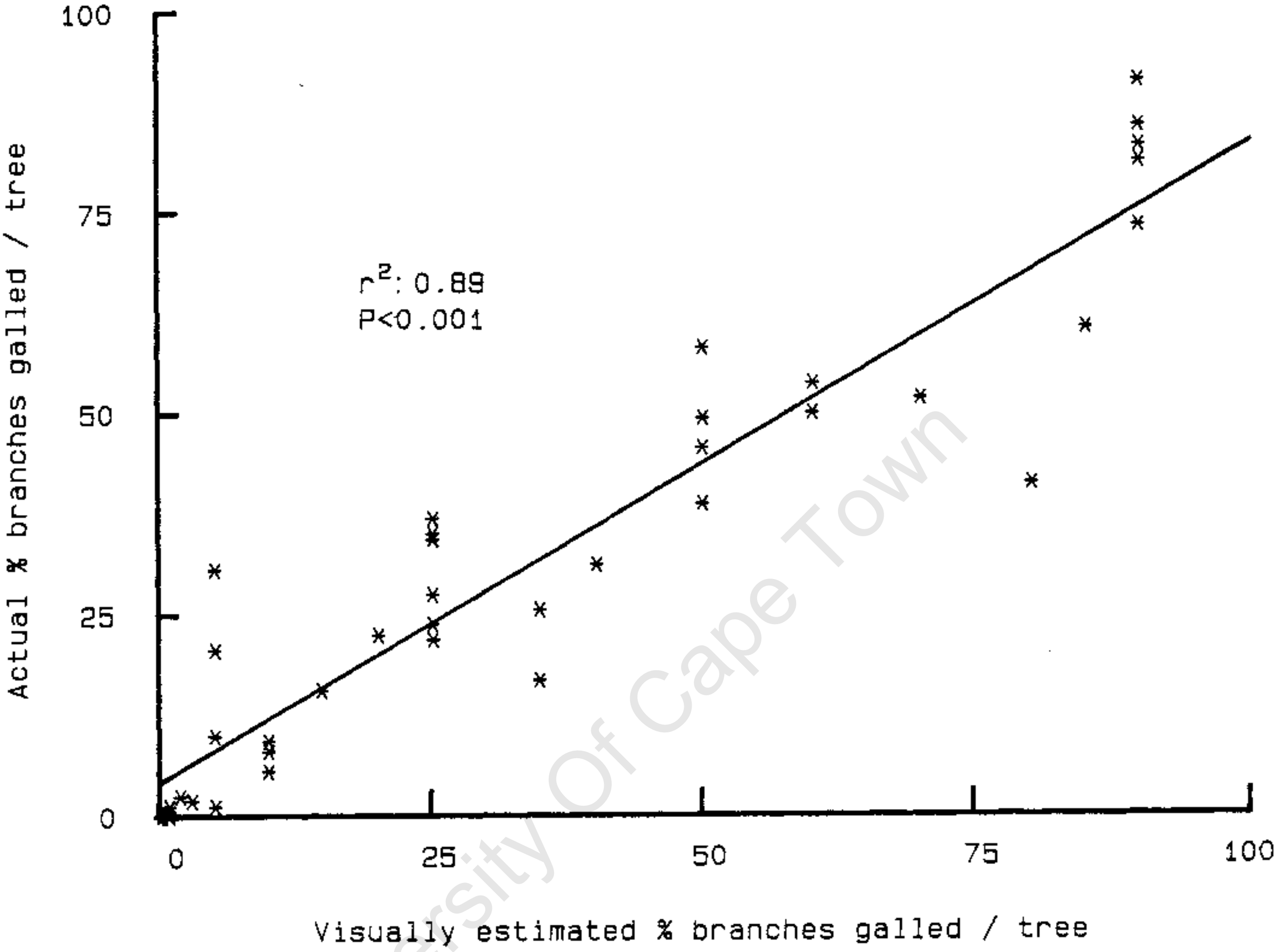


Fig. 3. The relationship between visually estimated and actual percentages of galled branches per *A. longifolia* tree. Regression equation: y = 4.068 + 0.805x.

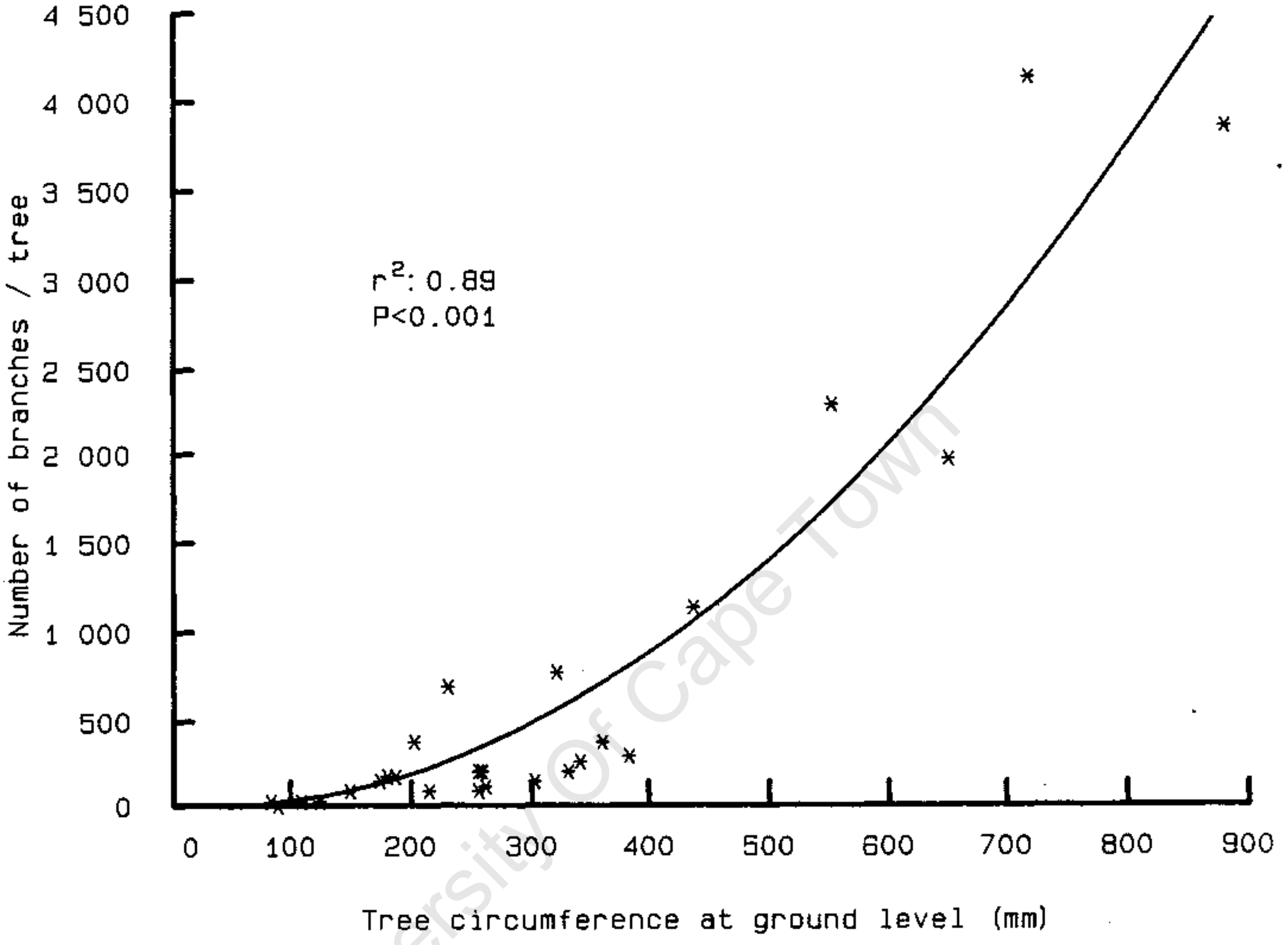


Fig. 4. The relationship between basal tree trunk circumference (mm) and number of branches for *A. longifolia* trees at Vergelegen and Banhoek. Regression equation: $y = -83.205 + 0.006x^4$.

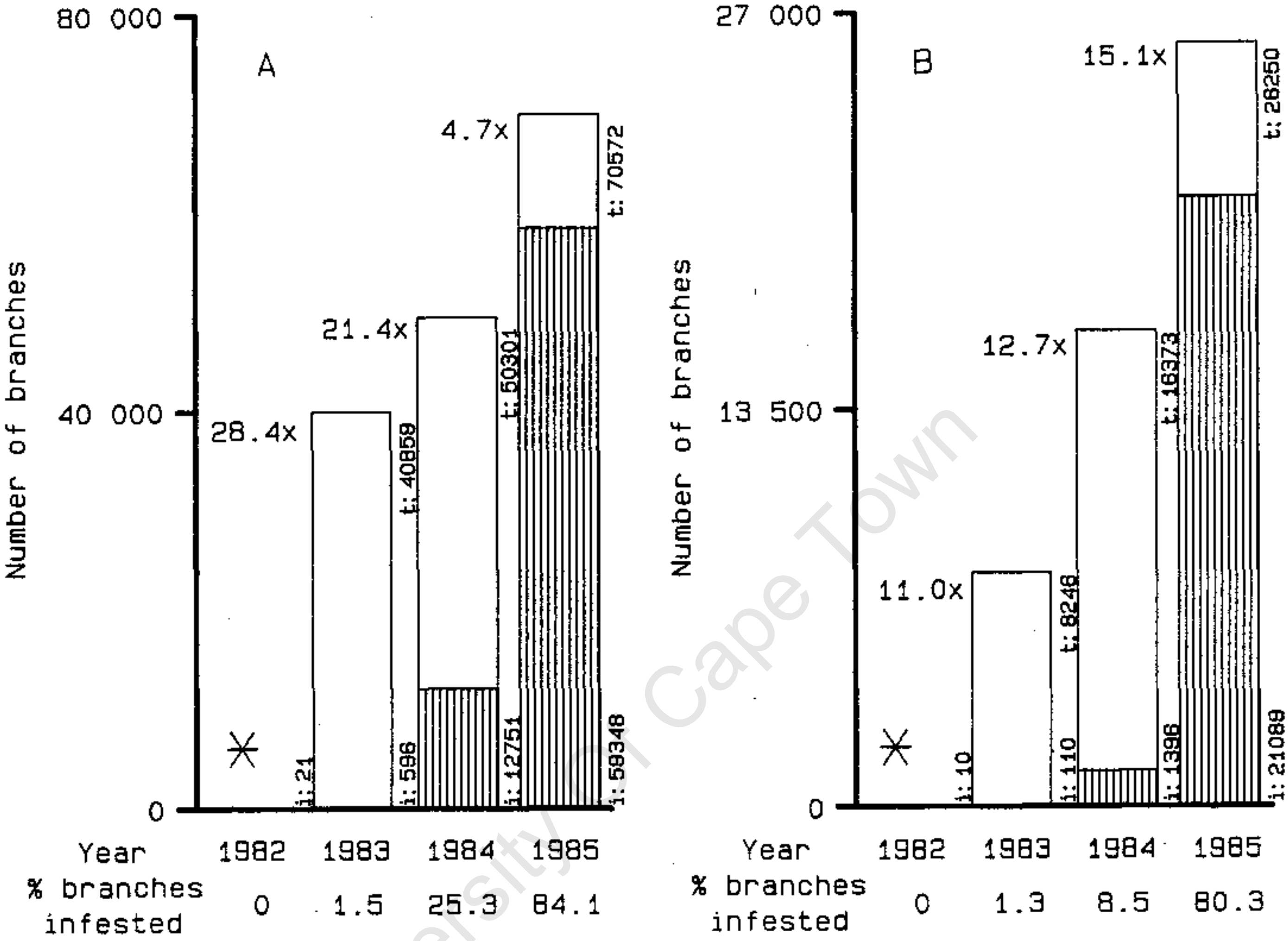


Fig. 5. Annual increases in the total number of branches on sample *A. longifolia* trees (t) and the number of branches galled by *T. acaciaelongifoliae* (shaded and indicated by `P) from 1982 (release generation = *) until 1985 at Vergelegen (A) and Banhoek (B). The multiples by which the number of galled branches increased annually are indicated by an x and given at the top of each histogram bar.

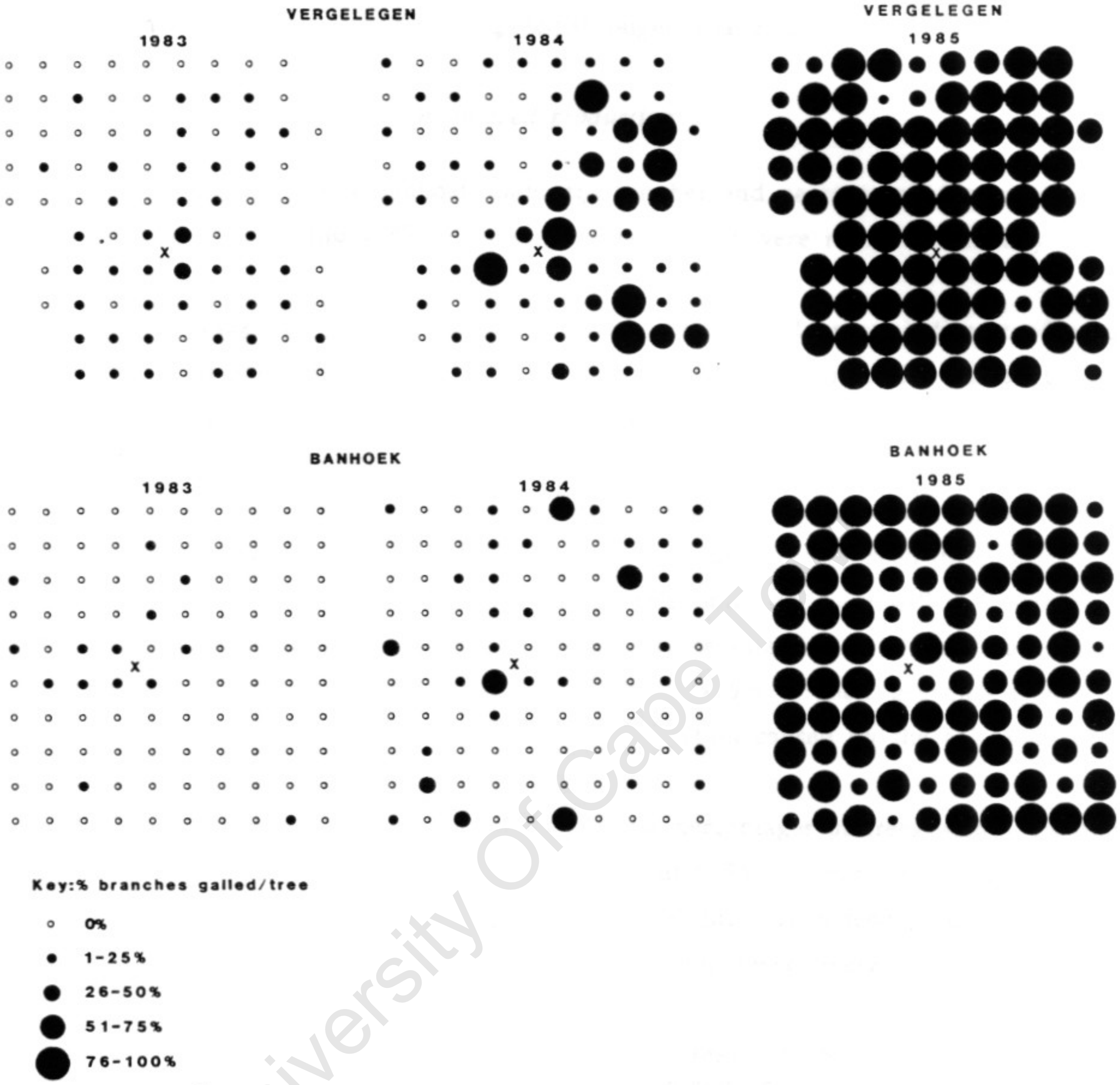


Fig. 6. The rate and pattern of dispersal of *T. acaciaelongifoliae* shown by illustrating annual levels of galling on marked trees on 100- by 100-m plots at Vergelegen and Banhoek from 1983 to 1985 (X = release points). Method of representation after Kluge (1983).

infestation levels were somewhat irregular in the plots at Vergelegen and Banhoek, and in 1985 when both plots were heavily galled throughout (Fig. 6).

Extensive estimations of reductions in seed production

At the Vergelegen and Banhoek plots, the number and percentage of marked trees which had 50 to 75% and >75% of their branches galled were recorded annually from 1983 to 1985.

The percentage of galled branches per tree can be used as an indicator of seed reduction. Pod and seed production of *A. longifolia* trees is inversely related to the proportion of galled branches on a tree (Chapter 2; Dennill 1985; Appendix 1). At Vergelegen, pod production of trees with >50% and >75% of their branches galled was reduced by 89% and 95% respectively (Chapter 2; Dennill, 1985; Appendix 1). At Eerste River, a riverine site where *A. longifolia* grows into large trees, seed production was reduced by >95% when as few as 50% of a tree's branches were galled (Chapter 2; Dennill, 1988b in press; Appendix 4). It is thus only necessary to determine the number or percentage of sampled trees which have >50% or >75% of their branches galled in order to quickly determine reductions in seed production caused by the gall wasp at a study site.

Within three generations of the gall wasp, the percentages of trees with >75% and 50 to 75% of their branches galled were 83% and 95%, and 73% and 91% for Vergelegen and Banhoek, respectively (Table 3). Reductions in seed production at the two sites are thus estimated at 83 to 95% and 73 t9 91%, respectively.

TABLE 3 The percentage of sampled *A. longifolia* trees with 50 to 75% and >75% of their branches galled on (100-m) plots at Vergelegen and Banhoek from 1983 to 1985.

Site	Year	50-75% branches galled / tree	>75% branches galled / tree
Vergelegen	1982	Release	Release
	1983	0.0	0.0
	1984	17.6	8.2
	1985	95.3	83.5
Banhoek	1982	Release	Release
	1983	0.0	0.0
	1984	6.0	0.0
	1985	91.0	73.0

Number of gall wasps developing per gall

When adult emergence had ceased in midsummer 1983, 816 galls were sampled at various heights from 20 trees which ranged in galling intensity from 5 to 95% galled branches per tree. These galls were grouped into five classes according to the number of chambers per gall. For each gall the number of emergence holes was counted. Then the galls were dried at 60 °C for three days and their dry weight was measured.

Although there was an overall 24% decrease in the number of *T. acaciaelongifoliae* produced per chamber with increasing number of chambers per gall, the number of wasps produced per gram of gall dry weight increased by 18% with increasing number of chambers (Table 4).

TABLE 4 The number of *T. acaciaelongifoliae* maturing per chamber and per gram of gall dry mass for galls comprised of varying numbers of chambers, and the frequency distribution of the galls composed of different numbers of chambers. Tukey's D value (P=0.05) for comparing dry weights of the galls in each class = 0.203.

Parameter	**Number of cells/gall**				
	1	2	4	5	>5
Mean dry mass (g)	0.496	0.833	1.089	1.389	1.697
% galls	33.5	30.3	21.2	10.0	5.1
No. galls (n)	273	247	173	82	41
No. wasps/cell	1.05*	0.96	0.84	0.88	0.80
No. wasps/g	2.08	2.18	2.32	2.53	2.54

The reason for there being an average of 1.05 wasps/cell for single-chambered galls is the occasional occurrence of a tiny second chamber which is externally invisible on a gall which otherwise appears single-chambered.

Sex ratios and incidence of parasitism

During October (spring) of 1984 and 1985, samples of galls (n=400 to >2000) were picked from 40 trees at each of five sites where releases had been made in spring 1982. These sites were Vergelegen, Banhoek, Eerste River, Stellenbosch and Franschhoek. The picked galls were placed in emergence boxes and the number of ***T.***

acaciaelongifoliae **males and females and other insects that emerged were counted. The latter were sent to specialists for identification.**

The sex ratio of *T. acaciaelongifoliae* females per male varied between 1.6 and 11.1 but averaged 5.3 for the five sites monitored in 1984 and 1985 (Table 5). The percentage co-emergence of insects other than *T. acaciaelongifoliae* (Hymenoptera only) from the galls picked at the five sites that were monitored was consistently low, averaging 0.5% and not exceeding 1.6% (Table 5). The taxa were able to be identified only to generic level as *Antistrophoplex* sp. and *Torymus* sp. Although these species are parasitic, it is not known whether they parasitise *T. acaciaelongifoliae.*

TABLE 5 Sex ratios and incidence of co-emergence of other Hymenoptera from *T. acaciaelongifoliae* galls picked at five sites in the south western Cape Province.

Site	Year	% Co-emergence	No.galls	Sex ratio
Eerste River	1984	0.14	2088	6.0:1
	1985	0.29	2094	5.8:1
Stellenbosch	1984	0.42	472	1.6:1
	1985	1.64	733	3.5:1
Banhoek	1984	0.45	2000	6.4:1
	1985	0.24	1226	3.6:1
Franschhoek	1984	0.50	2014	11.1:1
	1985	0.14	2142	4.1:1
Vergelegen	1984	0.43	700	6.4:1
	1985	0.89	1346	4.9:1

Location and utilisation of reproductive buds

At Vergelegen, 1092 galled branches were selected at various heights on 30 trees in October 1983. The branches were placed in two categories: those with galls in their apical 30-cm segments and those with galls on the proximal parts of the branch but with no galls on the apical 30-cm segments.

In October 1984, 100 and 200 galled trees were examined at Eerste River and Vergelegen, respectively. Those trees with noticeable quantities (>25%) of their galled branches lacking galls in their apical 30-cm segments were counted.

At Stellenbosch, 100 trees were selected in a dense (1 to 2 trees/m^2) stand of tall *A. longifolia* trees (max. height 7 m). One tree was selected every five meters on 10

transects which were five meters apart. Each tree was cut down and divided into 1-m zones above ground level. The number of branches and number of galled branches in each zone were determined.

Of the 1092 galled branches sampled at Vergelegen, only 6.1% did not have galls in their apical 30-cm segments. The percentages of the 100 and 200 trees with >25% of their galled branches lacking galls in their apical 30-cm segments were only 2.0% and 3.5% at Eerste River and Vergelegen, respectively.

The distribution of galled branches on tall *A. longifolia* **trees at Stellenbosch Mountain was similar to that of the general distribution of branches on the trees (Fig. 7). In the 3-4, 5-6 and 6-7 m zones, however, the proportion of galled branches was significantly greater than that of the proportion of branches, indicating that gall wasp attack was relatively higher in the upper growing parts of the trees. These upper parts of the trees are more exposed to sunlight and tend to bear more inflorescences (Milton, 1980). There were no galls in the bottom 1-m zone since the branches in this zone were all dead. The proportion of galled branches in the 1-2 m zone was significantly lower than that of the proportion of branches. This is explicable because the lower branches in such** *A. longifolia* **thickets senesce and bear fewer inflorescences because of the relative lack of sunlight.**

Gall loss and wasp survival from spring to summer

At Vergelegen and Banhoek in 1985, 200 and 100 branches with one or more galls on them were marked on 40 and 20 trees, respectively (5 branches/tree). The galls on each branch were counted at the beginning of September (spring) when the developing galls were clearly visible, and in late November (summer) when the galls were mature.

At Eerste River, Banhoek and Vergelegen in 1983, samples of 4282, 3438 and 330 galls were picked from 100, >50 and 11 trees, respectively. These galls were sampled in December immediately after emergence had ceased. The number of individual gall cells from which wasps did not emerge (signifying failure to complete development to the adult phase) was determined for each sample.

At Vergelegen the total number of galls on the sampled branches decreased from 2405 to 2086 (13.3%), and the mean number of galls per branch decreased from 12.0 to 10.5%. At Banhoek, the total number of galls decreased from 1450 to 1202 (17.1%) and the mean number of galls per branch decreased from 14.5 to 12.7. The loss of

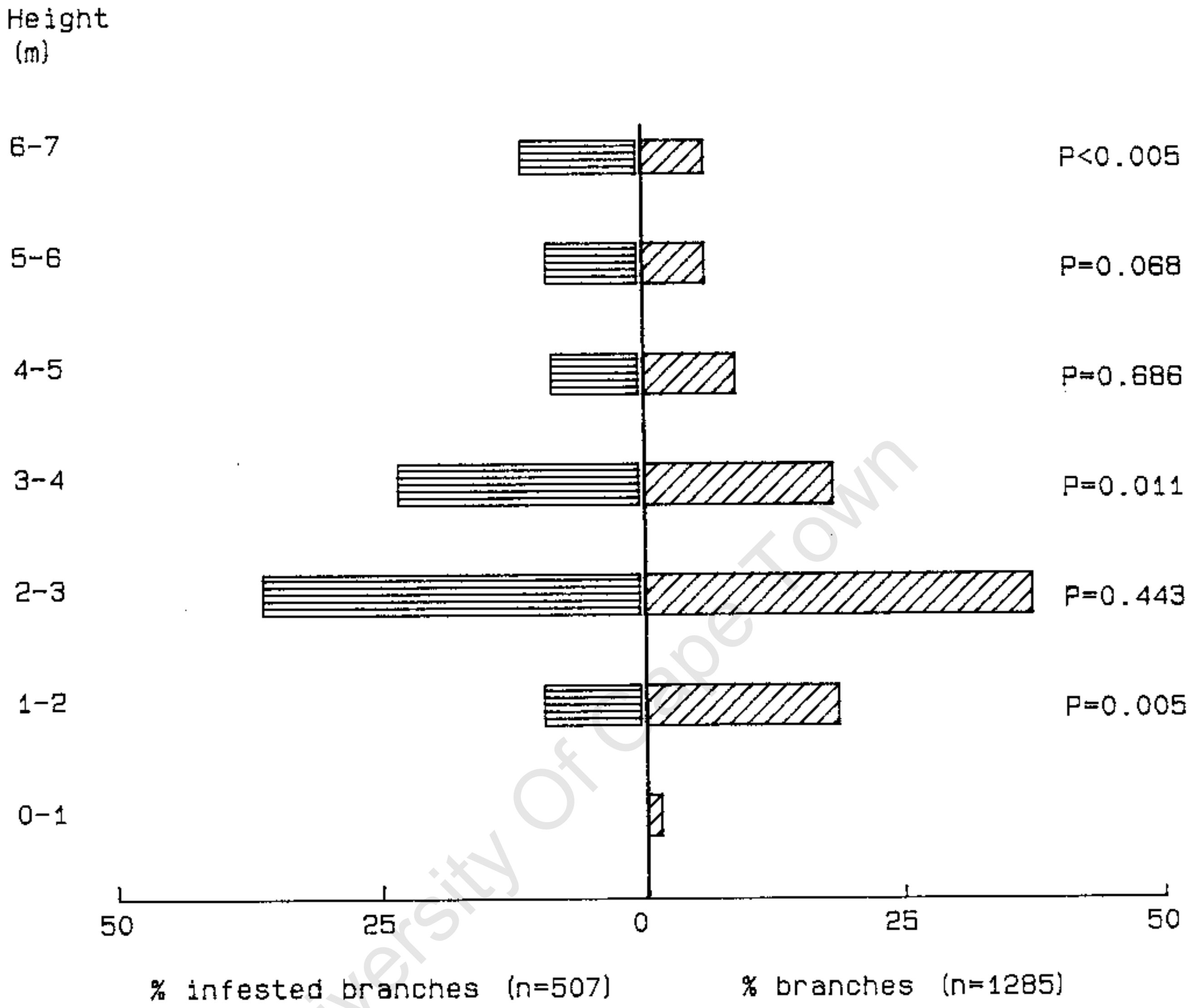


Fig. 7. Comparison of the vertical distribution of branches in a stand of tall and dense *A. longifolia* trees at Stellenbosch with the vertical distribution of galled branches on these trees. The probability values for Chi-Square tests for each of the vertical 1-m zones are indicated.

developing galls between spring and mid-summer is attributed to branches abrading each other during the windy summer months.

The percentages of individual gall cells from which wasps did not emerge *(i.e. %* wasps failing to develop to adult phase) at Vergelegen, Banhoek and Stellenbosch, were 15.7%, 22.7% and 28.8%, respectively.

Correlation of number of chambers/gall with decreasing levels of infestation at increasing distances from release point

A series of six groups of six trees was selected at Vergelegen in October 1985. The six trees of the first group were all located within 10 m of the release point and all had about 90% of their branches galled. The 2nd, 3rd, 4th, 5th and 6th groups of trees were selected on five hypothetical circles around the release point such that the trees from the innermost to the outermost circles had approximately 80, 60, 40, 20, and 1% of their branches galled, respectively. The circles were 15 to 20 m apart. Five galled branches were randomly selected at a height of 1.0 to 1.5 m from each tree in each group. All the galls were picked off the 30 branches from each group of trees and those galls with one and two chambers were counted separately from those with three or more chambers.

There was a significant positive linear trend for the proportion of one- and two-celled galls to increase with decreasing infestation levels at increasing distances from the release point ($P < 0.0001$) (Fig. 8).

DISCUSSION

The growth rates of the *T. acaciaelongifoliae* populations at Vergelegen and Banhoek were much greater than those of the *A. longifolia* trees. This resulted in an increase in the percentage of galled branches and a decrease in pod and seed production which were as impressive as the exponential increases in the wasp populations.

As has already been stated, the loss of developing galls between spring and summer when the adult wasps emerge is attributed to the branches abrading each other during the windy summer months. Although as many as 17% of the galls may get broken off the branches, and up to 28% of the wasps in surviving galls may not develop to the adult phase, this did not retard the rapid growth of the *T. acaciaelongifoliae* populations at Vergelegen and Banhoek. Parasitism has been shown to be negligible if it occurs at all. Apart from the fact that the gall wasp was introduced without its natural

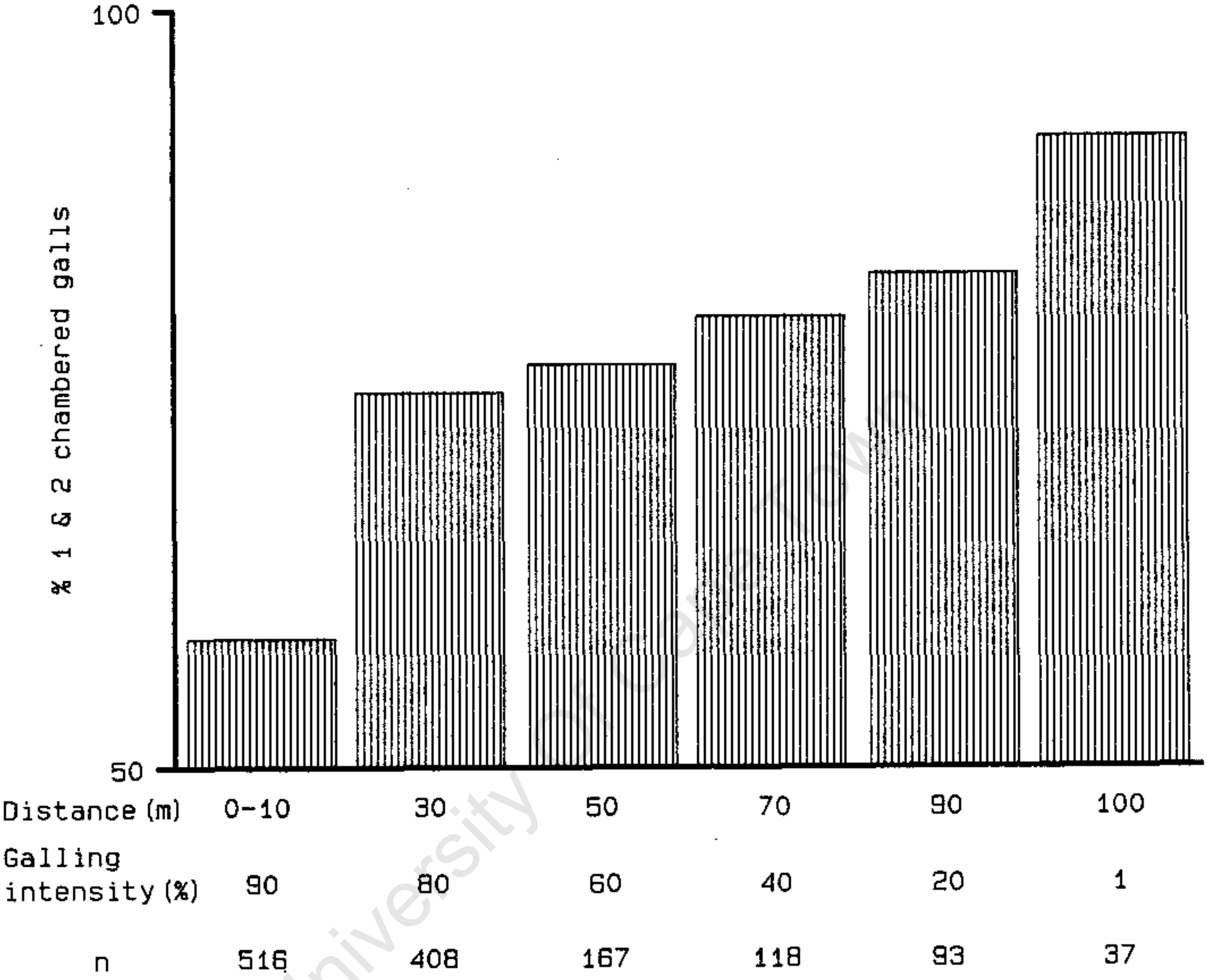


Fig. 8. The relationship between the proportion of one- and two-chambered galls with decreasing intensities of galling by *T. acaciaelongifoliae* at increasing distances from the release point at Vergelegen.

enemies, and the low incidence of parasitism of the wasp in South Africa, there are a number of other important reasons for the phenomenal population growth rates.

Firstly, female *T. acaciaelongifoliae* are highly fecund. The average number of eggs per newly hatched female is 409.8 (Noble, 1940). Secondly, despite the short duration of the adult phase (average 2.3 days), the females are parthenogenetic and oviposition can commence immediately (Noble, 1940). No time need be spent on locating a mate. Thirdly, the parthenogenetic females tend to outnumber males. Since the females on their own are the actual biological control agents, it is obviously beneficial that relatively few galls are spent producing males. Fourthly, the high productivity of multiple-chambered galls also contributes to the population growth. Multiple galls constitute about 66% of the galls, and if gall wasp survival rate decreased significantly (due, *e.g.* to competition) with increasing number of chambers per gall, this could have a detrimental effect on the population growth of the wasp. In terms of plant material converted into wasps, the multiple-chambered *T. acaciaelongifoliae* galls are in fact more productive than single-chambered galls.

Given an abundance of *A. longifolia* buds in which to oviposit, *T. acaciaelongifoliae* females tend to lay fewer eggs per bud and per branch as they disperse, thus producing scattered single- and double-celled galls. This behaviour accounts for the initial patterns of dispersal at Vergelegen and Banhoek, in which the highest concentrations of galls were located around the release points. The large populations increased proportionately the rate of dispersal of the wasps, resulting in high infestation levels at points scattered throughout the study sites in 1984 and 1985.

Females that have laid eggs for a few hours begin to fly, especially as daily temperatures increase, and exhibit strong, directed flight (Neser, 1985). In 1984 & 1985, second generation galls were found on trees up to 20 km from release points in the south-western Cape Province. Wind dispersal is apparently responsible for the large distances covered, and, coupled with excellent flying and host seeking ability, results in successful establishment of remote colonies.

The combined result of all of the features discussed above was a large reduction in the reproductive potential of the *A. longifolia* populations by the gall wasp. Reductions in seed production retard the rate at which any plant spreads (Harper, 1977). The large seed reductions caused by *T. acaciaelongifoliae* will thus markedly limit the invasiveness of *A. longifolia.* Observations at release sites other than those studied here indicate that establishment and levels of infestation are similarly impressive (see Chapter 5). In addition to the effects of the wasp on reproductive potential, the suppressive effects it

has on vegetative growth of *A. longifolia* (Chapter 2; Dennill 1985; Appendix 1) will result in significant and large scale reductions in biomass of the adult weed populations.

The results reported in this chapter show that *T. acaciaelongifoliae is* an ecologically successful biological control agent since it established remarkably well under South African conditions. In addition, an indication has been given that the wasp is successful in accomplishing the purpose for which it was introduced, namely reduction of seed production by *A. longifolia.* In the next chapter it will be shown that an additional advantage of a gall forming agent like *T. acaciaelongifoliae is that* it is able to markedly suppress the vegetative growth of its host while simultaneously accomplishing the reduction of its host's reproductive potential.

CHAPTER 2

The effect of the gall wasp *Trichilogaster acaciaelongifoliae* on reproductive potential and vegetative growth of the weed *Acacia longifolia*

ABSTRACT

Comparison of branches from heavily galled trees (those with >75% of their branches galled) and ungalled *A. longifolia* trees shows that the gall wasp *T. acaciaelongifoliae* reduced seed production of *A. longifolia* by 85 to 100% (mean 96%) at five sites in the south-western Cape Province. Pod production of trees was inversely related to the proportion of galled branches and was reduced by an average of 89% to 95% when >50% of the branches on a tree were galled, irrespective of tree size. Reduction in seed production was achieved directly by galling of reproductive buds and indirectly by increased abscission of inflorescences on galled branches. Galls caused phyllode abscission, reduced lateral branching by 66% and increased shoot tip mortality to 100% by midsummer. The overall reduction in vegetative growth was 53% by midsummer. After adult emergence in mid-summer the galls desiccated, resulting in recovery of galled branches, but growth of these branches was still reduced by 30% eight months later.

The aim of the studies reported in this chapter was to determine the potential of *T. acaciaelongifoliae* for the reduction of seed production and growth of *A. longifolia.* Branches from galled trees were compared with branches from ungalled trees to determine the effects of galling on inflorescence, pod and seed production and vegetative growth. The effects of varying intensities of galling on the seed production of whole trees was also examined. These data have been published by Dennill (1985) (Appendix 1).

METHODS AND RESULTS

During December 1981, 217 *T. acaciaelongifoliae* were caged in 21 gauze sleeves each containing about 10 living branches of *A. longifolia* at Vergelegen *(ca* 10 females/sleeve), and 48 females were similarly caged in 10 sleeves at Banhoek Mountain *(ca* 5 females/sleeve). The caged wasps were allowed to lay eggs and the gauze sleeves were removed a week later when all the short-lived adults had died. The following year the progeny of the first generation emerged and dispersed naturally. In 1982, 723 female *T. acaciaelongifoliae* were liberated at Eerste River outside Stellenbosch. The studies reported in the present chapter were done at these three sites, namely Vergelegen, Banhoek Mountain and Eerste River. Data collection at each site

commenced only during the galling caused by the second *T. acaciaelongifoliae* generation after release.

Since *T. acaciaelongifoliae* was introduced to stop *A. longifolia* from flowering, inflorescence distribution was used as a basis for sampling. About 78% of the inflorescences on a tree were located in the outer 30-cm segments of the branches (Table 6; Plate 3). In a sample of 40 branches similarly examined in 1984, 95% of the inflorescences were located in the outer 30-cm segments. Unless otherwise stated, the term 'branch' is used to signify the outer 30-cm segment of a branch.

TABLE 6 Distribution of the inflorescences on *A. longifolia* branches (based on 60 branches randomly selected from 31 ungalled trees) at Vergelegen in 1983.

	Sequential branch segment from tip (1) to trunk (4)			
	1	2	3	4
Number of inflorescences (Total = 2709)	2111	578	20	0.0
Mean/segment	35.2	9.6	0.3	0.0
% / segment	77.9	21.3	0.8	0.0

Comparison of inflorescence, pod and seed production of galled and ungalled branches

At Vergelegen in 1983, 14 galled trees which displayed the highest levels of attack (>75% of their branches galled) were selected. In September, 60 branches with one or more galls were randomly selected and labelled on these trees (Plate 3). Of the 60 branches, 20 were selected at each of three heights, namely 1.0, 1.5 and 2.0 m. Sixty ungalled branches selected similarly from 31 ungalled trees served as controls (Plate 3). Numbers of inflorescences and pods on marked branches were counted monthly. Ripe pods were picked in November and the seeds counted. Similar recordings were made on an additional 23 branches which, although galled, had no galls in their apical 30-cm segments. (Only 23 branches of this type could be found.)

A similar study was done in 1983 at Banhoek Mountain on 40 galled and 40 ungalled branches which were similarly selected from 11 galled and 20 ungalled trees, respectively.

Plate 3

Top. An ungalled *A. longifolia* branch (top) photographed in spring (September) when the branches are laden with inflorescences, most of which are located in the apical 30-cm segment (marked here by a string label).

Bottom. An *A. longifolia* branch that has been galled by *T. acaciaelongifoliae*, and which consequently shows an abscence of inflorescences on the apical 30-cm. This photograph was also taken in spring (September).

In order to determine the effects of galling on seed production at a wider range of sites, branches were marked in the same way at Vergelegen, Banhoek River and Eerste River in 1984. The number of branches compared at each site ranged from 40 to 60 and were selected from 10 to 22 galled or ungalled trees. At Eerste River, however, levels of galling were so high that no control trees could be found. The branches thus marked in 1984 were used to compare final seed production of galled and ungalled branches in November. In addition, these branches were used, with those from Vergelegen and Banhoek Mountain in 1983, to compare the percentage of inflorescences which abscised between spring (August/September) and pod maturation in summer (November) on galled and ungalled branches.

There was a natural loss of inflorescences and pods from ungalled branches averaging 63.1% at Vergelegen (Table 7) and 58.1% at Banhoek Mountain (Table 8). However, the loss of inflorescences was much greater on galled branches, leading eventually to reductions in the number of seeds per branch of 99.3% at Vergelegen (Table 7) and 85.3% at Banhoek Mountain (Table 8). The difference in inflorescences per branch at the beginning of the study in September was already highly significant (LSD[0.01] = 4.0 for Vergelegen ; LSD[0.01] = 11.5 for Banhoek Mountain), and increased until final evaluation on November 17th and 21st when the last samples were taken at Vergelegen and Banhoek, respectively. The average number of seeds per branch (25.9) for the 23 Vergelegen branches with galls internal to their apical 30-cm segments was reduced by 74.2%.

TABLE 7 Monthly comparison of inflorescence, pod and seed production of galled *A. longifolia* **branches with branches from ungalled trees at Vergelegen from September until 17 November 1983 when the pods were picked. U = ungalled branches ; G = galled branches ; * = pods too small to be counted.**

		Sept.	Oct.	Nov.	17 Nov.
Inflorescences/ branch	U	35.2	15.7	13.0	13.0
	G	4.4	0.2	0.2	0.2
Pods/branch	U	*	22.0	17.5	16.7
	G	*	0.2	0.2	0.2
Seeds/branch	U				100.3
	G				0.7

TABLE 8 Monthly comparison of inflorescence, pod and seed production of galled A. *longifolia* branches with branches from ungalled trees at Banhoek from September until 21 November 1983 when the pods were picked. U = ungalled branches ; G = galled branches ; * = pods too small to be counted.

		Sept.	Oct.	Nov.	17 Nov.
Inflorescences/ branch	U	38.9	23.0	15.6	16.3
	G	20.8	3.6	2.5	2.5
Pods/branch	U	*	38.4	22.4	22.4
	G	*	4.1	3.0	3.0
Seeds/branch	U				96.8
	G				14.2

Similarly impressive reductions in seed production caused by galling were noted at all study sites (Table 9) and averaged 96.1 ± 2.8%. Abscission of inflorescences on galled branches (96.1%) was substantially greater than that on ungalled branches (62.7%) (LSD[0.05] = 9.7) (Table 10).

TABLE 9 Comparison of seed production of galled A. *longifolia* branches with branches from ungalled trees at various sites in the south western Cape Province in 1983 and 1984. U = ungalled branches ; G = galled branches ; * = no control trees found because galling intensity was so high.

Site/ year	Site type	No.seeds/branch		% seed reduction
		U	G	
Vergelegen 1983	Non-riverine: Shrubs and small trees	100.3	0.7	99.3
Banhoek Mountain 1983	"	96.8	14.2	85.3
Vergelegen 1984	"	37.9	0.0	100.0
Banhoek River 1984	Riverine: Large trees	107.1	3.8	96.5
Eerste River 1984	"	*	0.0	100.0

TABLE 10 Comparison of the proportion of inflorescences abscising on galled *A. longifolia* branches and branches from ungalled trees over the period from September (spring) to November (summer) at various sites in the south western Cape Province in 1983 and 1984. U = ungalled branches ; G = galled branches ; * = no control trees found because galling intensity so high.

Site/year		No.inflorescences/branch		% abscission
		September	November	
Vergelegen 1983	U	35.2	13.0	63.1
	G	4.4	0.2	95.5
Banhoek Mountain 1984	U	38.9	16.3	58.1
	G	20.8	2.5	88.0
Vergelegen 1984	U	15.2	4.1	73.0
	G	0.1	0.0	100.0
Banhoek River 1984	U	31.1	13.5	56.6
	G	19.5	0.6	96.9
Eerste River 1984	U	*	*	*
	G	0.0	0.0	100.0

Effect of number of galls per branch on (a) inflorescence production and (b) branch tip mortality

In September 1983, 106 galled branches sampled at Vergelegen were used to correlate number of galls per branch with inflorescence production per branch. The branches had one or more galls, and were selected in the same way as described above from trees with 50 to 100% of their branches galled. These branches were grouped into four classes according to number of galls (1-10, 11-20, 21-30 & >30 galls/branch respectively), and the proportion of branches with dead branch tips was calculated for each class.

When this study was initiated (September 1983), correlation between the number of galls and number of inflorescences per branch was low ($r = -0.50$) although it was significant ($P < 0.001$), and polynomial regressions fitted relatively poorly ($r^2 < 0.30$, $P < 0.001$). At that stage, however, there was a strong positive linear trend for the proportion of dead growth tips to vary with the category of of gall numbers ($P < 0.001$)

(Fig. 9). By the time the pods were harvested, branch tip mortality (see Fig. 11D) and seed production per branch (Table 7 above) were as adversely affected by one as by many galls.

Effect of galling on vegetative growth

For the 60 galled and 60 ungalled branches marked at Vergelegen in 1983, the following were counted monthly from September 1983 until August 1984: (a) the number of phyllodes on the original 30-cm segment, (b) the number of nodes and phyllodes added by apical growth, (c) the number of side shoots added, and the total number of phyllodes added by such growth. The growth tip of each branch was recorded as dead or alive, and the number of individual galls developing on each galled branch was recorded.

For the 40 galled and 40 ungalled branches marked at Banhoek Mountain in 1983, the total number of phyllodes per branch (including phyllodes added by apical or lateral growth) and the number of side-shoots were counted in October and November 1983 and thereafter in January, May and August 1984. This was done to determine whether the effects of galling were similar at different sites.

In August 1984, the marked branches at both Vergelegen and Banhoek were cut off the trees. The desiccated galls of the previous summer were removed from the galled branches since this tissue was dead. The dry weights of the ungalled and galled branches (without the dead gall tissue) were then determined after drying the branches at 60°C for three days.

There was already a significant reduction in the number of phyllodes on galled branches of *A. longifolia* by spring (September) 1983 at Vergelegen (LSD[0.01]: (Fig. 10). The number of phyllodes on ungalled branches increased over the period of study (Fig. 10). However, the number of phyllodes on galled branches decreased until December 1983, and then began to increase after the previous season's galls had desiccated (Fig. 10).

A more detailed comparison of the growth of galled and ungalled branches over the period from September 1983 until February 1984 explains these results. The increasing number of phyllodes on ungalled branches is attributed to a lower incidence of phyllode abscission on the original 30-cm branch segments than on galled branches (Fig. 11A), and to the addition of phyllodes to the original 30-cm segments by both apical growth (Fig. 11B) and lateral branching (Fig. 11C). The presence of the galls on galled branches increased phyllode abscission on the original 30-cm segment (Fig. 11A), stopped apical

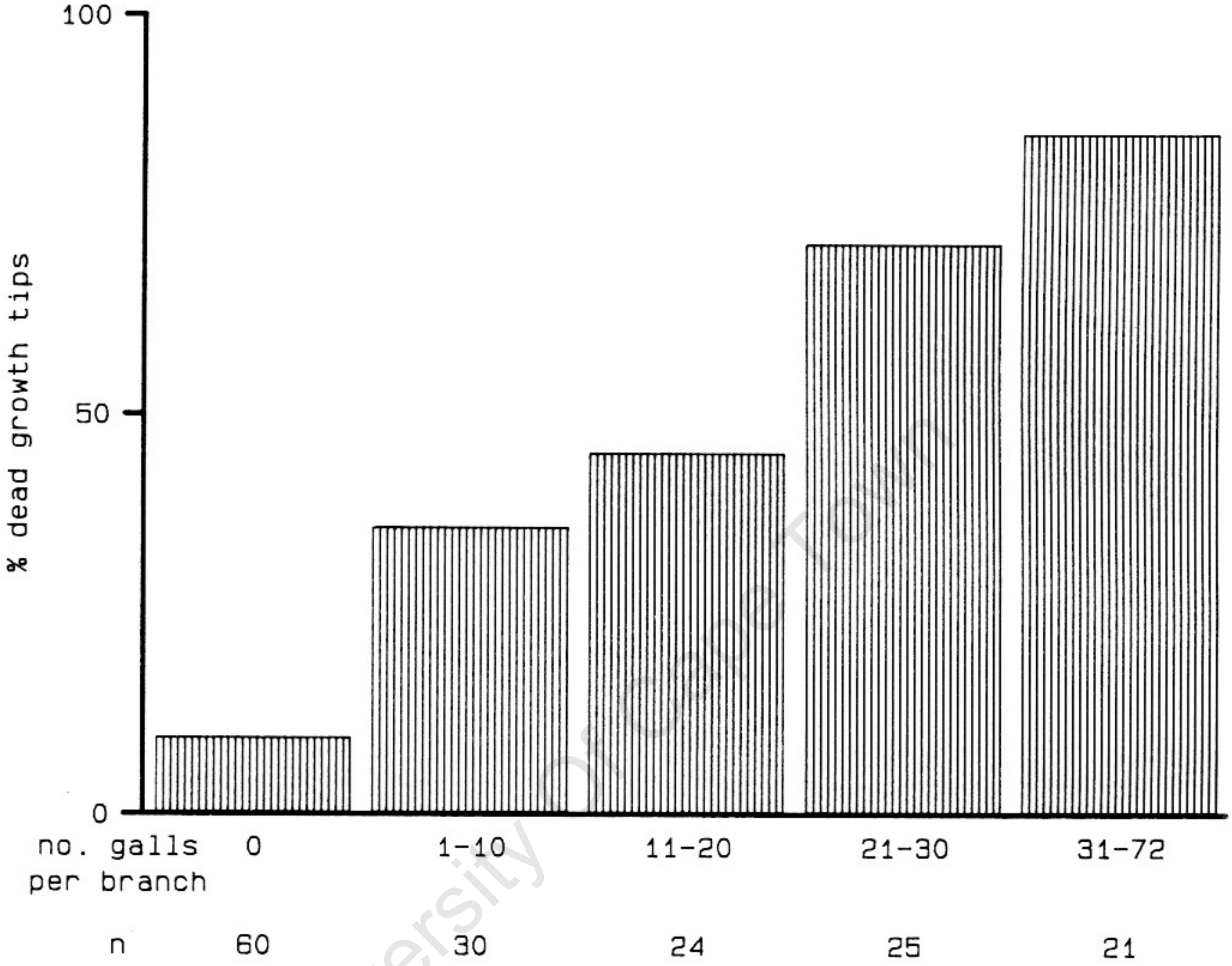


Fig. 9. The effect of varying numbers of *T. acaciaelongifoliae* galls per branch on the mortality of *A. longifolia* branch tips.

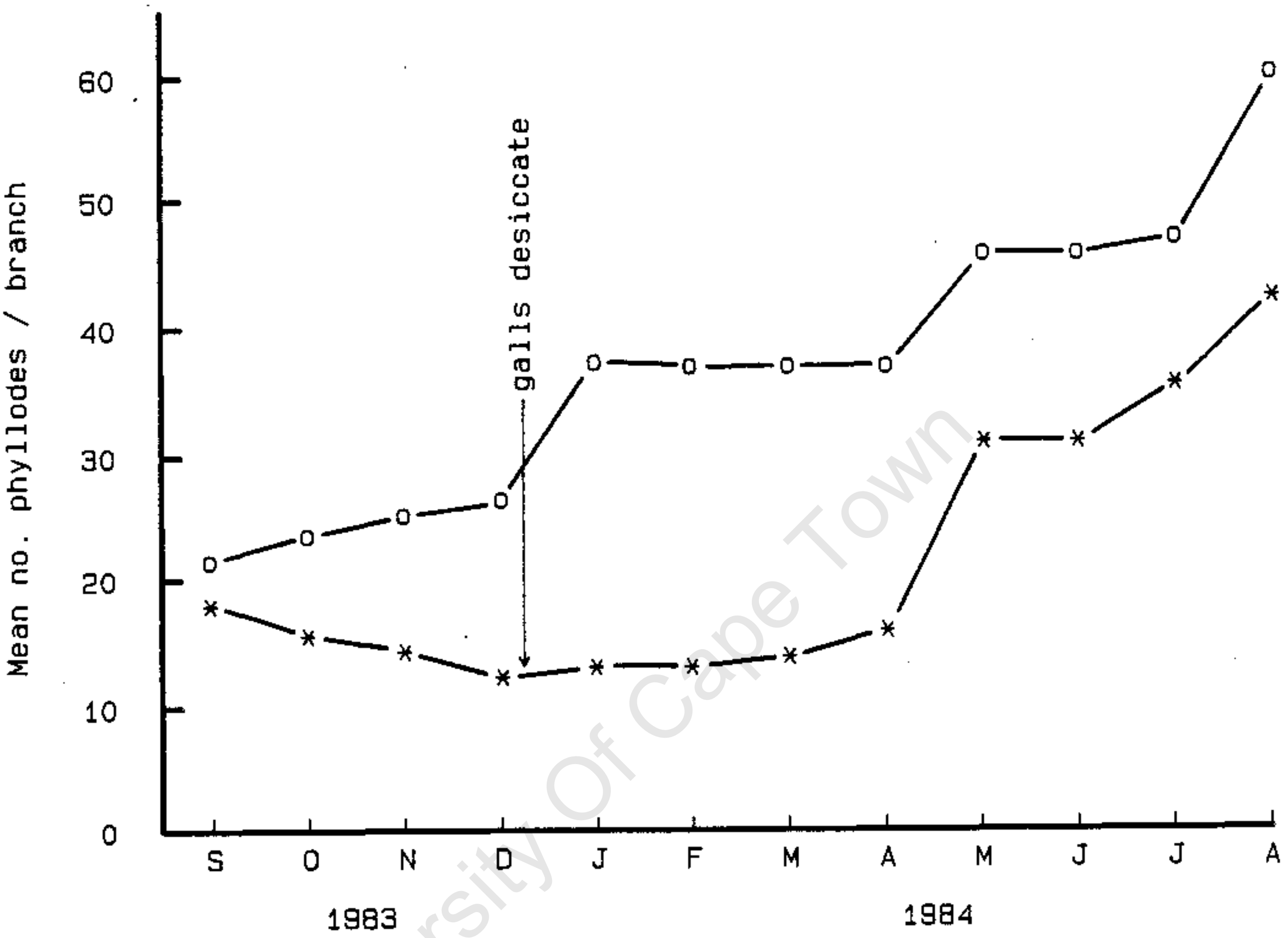


Fig. 10. Monthly variations in the mean number of phyllodes per branch for galled *A. longifolia* branches (*) and branches from ungalled trees (o) at Vergelegen. Phyllodes added by apical and lateral growth to the original 30-cm branch segments are included.

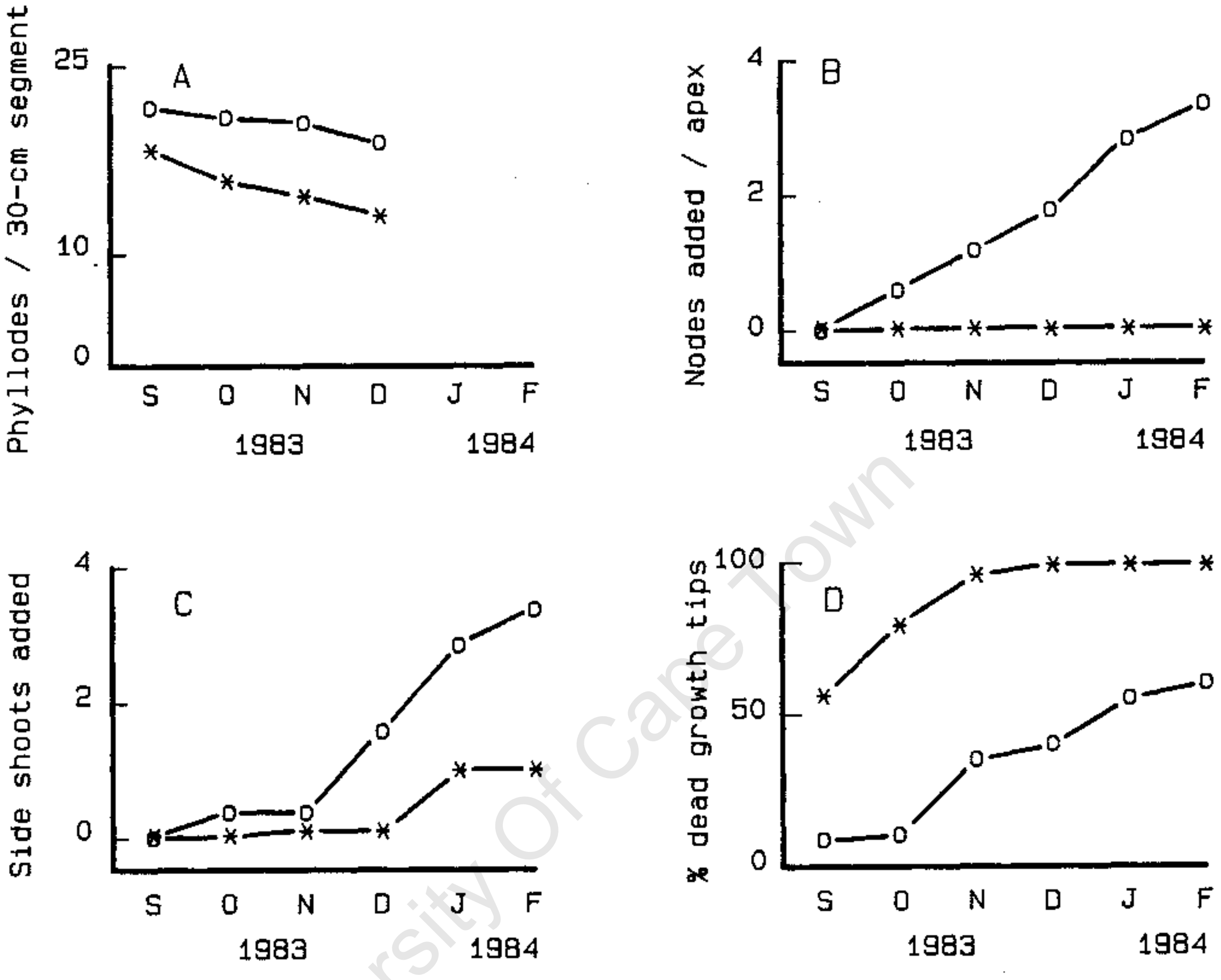


Fig. 11. Comparison of the vegetative growth of galled *A. longifolia* branches (*) and branches from ungalled trees (o) at Vergelegen from September 1983 until February 1984 : A. Number of phyllodes on original 30-cm branch segment, B. Number of nodes added per branch apex, C. Number of side-shoots added per branch, and D. Percentage dead growth tips.

growth (Fig. 11B) because the galls had increased growth tip mortality (Fig. 11D), and reduced lateral branching (Fig. 11C). Mortality of growth tips on ungalled branches (Fig. 11D) results in the death of only one or two apical nodes per branch but die-back caused by galling usually results in death of a number of nodes per branch.

Galling had similar effects on the growth of branches measured over one year at Banhoek Mountain (Fig. 12). At the beginning of the study in October 1983, the difference in number of phyllodes per branch between ungalled branches (19.9) and galled branches (12.5) was also significant (LSD[0.01] = 4.7). Galled branches had about half the number of phyllodes that ungalled branches had by December/January 1983/4 (Fig. 12).

By the end of January 1984 the wasps had all emerged, the galls had desiccated, and the plants could begin to recover by delayed lateral branching which accounted for the increase in phyllodes on galled branches at both sites (Figs. 10 & 12). However, in August 1984, eight months after the previous season's galls had ceased to directly affect the plants, galled branches still had significantly fewer phyllodes at both sites (29.6 to 35.3% fewer (P = 0.05)) (Figs. 10 & 12, Table 11), and their biomass was substantially reduced (by 28.3 to 35.7% (P 0.05)) (Table 11).

TABLE 11 Comparison of the number of phyllodes and dry weights of galled *A. longifolia* branches and branches from ungalled trees at Vergelegen and Banhoek Mountain in August 1984, eight months after wasp emergence and desiccation of the galls (these data apply to the last points on the graphs shown in Figs. 10 & 12). U = ungalled branches ; G = galled branches.

Site	No. phyllodes/branch		LSD [0.05]	% reduction
	U	G		
Vergelegen	60.2	42.4	8.8	29.6
Banhoek	32.3	20.9	10.0	35.3
	Mean dry weight			
	U	G		
Vergelegen	7.71	4.96	1.27	35.67
Banhoek	6.18	4.43	1.12	28.32

The annual growth flush, observed on both galled and ungalled branches, in Autumn (March and April) 1984 at Vergelegen (Fig. 10), is characteristic of *A. longifolia* (Milton, 1980).

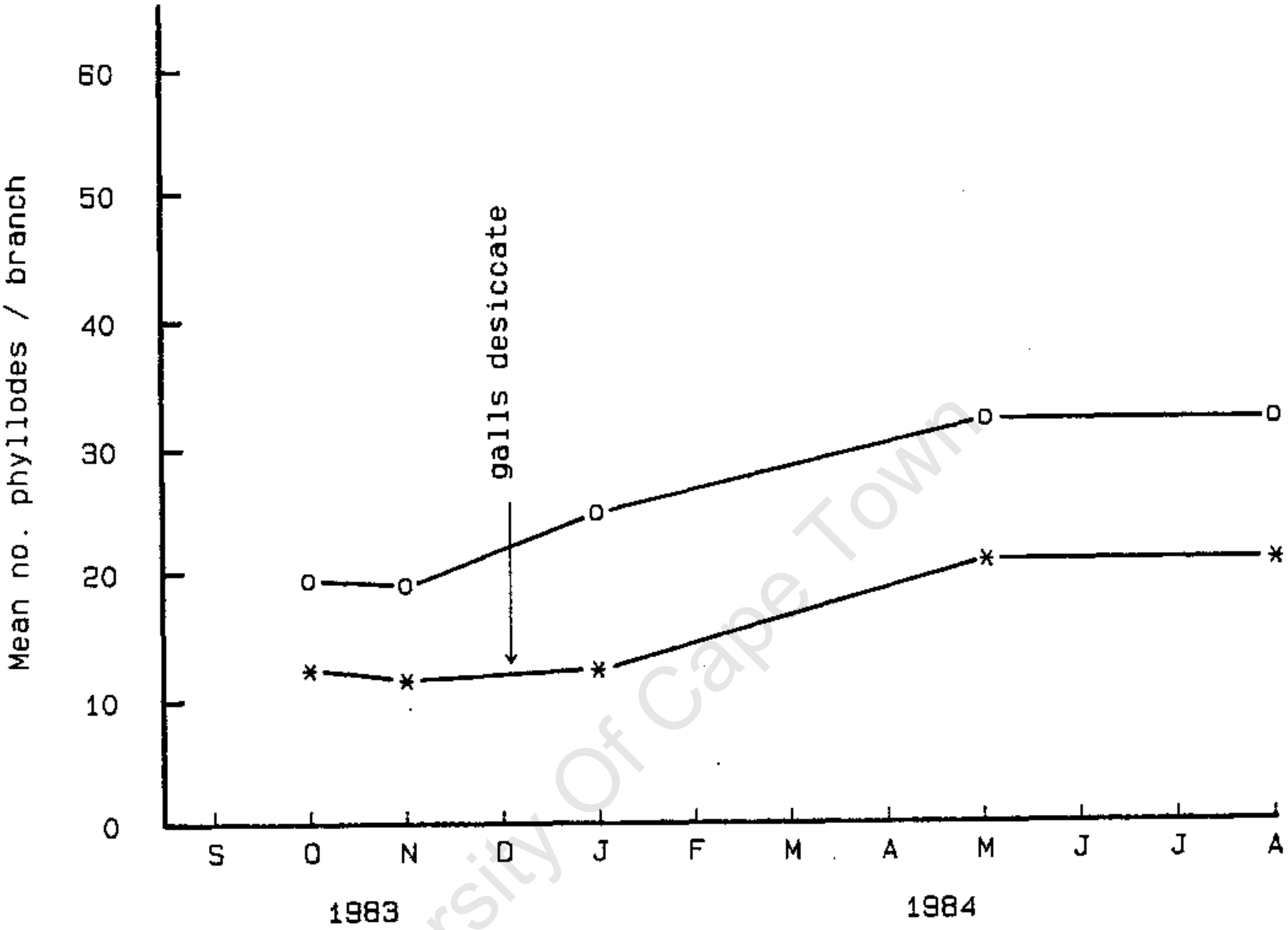


Fig. 12. Monthly variations in the mean number of phyllodes per branch for galled *A. longifolia* branches (*) and branches from ungalled trees (o) at Banhoek. Phyllodes added by apical and lateral growth to the original 30-cm branch segments are included.

Effect of galling on pod and seed production of whole trees

At both Vergelegen (in 1983) and Eerste River (in 1984) 16 trees of various sizes displaying various intensities of galling by the gall wasp were selected. The number of branches per tree ranged from 33 to 398 at Vergelegen where *A. longifolia* is shrub-like, and from 136 to 5616 at Eerste River where *A. longifolia* grows into large trees. The number of galled and ungalled branches were counted on each tree. All the pods were harvested from the trees, not just the pods in the outer 30-cm segments, and were counted. The seeds were also counted for the trees at Vergelegen but not for Eerste River since this would have been very laborious for these large trees, and since the pod counts yielded adequate data. Pod and seed production were corrected to tree size by dividing the number of pods and seeds by the number of branches. The percentage of galled branches per tree could thus be correlated with the pod or seed production per branch for each site.

At both Vergelegen and Eerste River, pod and seed production per branch decreased as percentage galled branches per tree increased (Figs. 13, 14 & 15). At Vergelegen in 1983 the average number of seeds per branch for trees with >50% of their branches galled was 3.6 compared with 31.8 for branches with <50% of their branches galled. This 89% reduction was significant (LSD [0.05] = 20.7). The lower coefficient of determination for percentage of branches galled and seeds per branch at Vergelegen (Fig. 14) is explained by variation among trees in the number of seeds per pod. At Eerste River, reduction in pod production of whole trees was similarly impressive ; trees with <40% of their branches galled produced 6.04 pods per branch whereas trees with >40% of their branches galled produced 0.65 pods per branch. This 89% reduction is also significant (LSD[0.05] = 3.84).

DISCUSSION

The results of these studies indicate that the gall wasp can dramatically reduce the reproductive potential of A. *longifolia* trees at sites representing a range of situations in which this plant is invasive. The wasp reduced seed production both directly by galling reproductive buds and indirectly by increasing abscission of the remaining inflorescences. The effect of the gall wasp on the selected galled trees used for branch comparisons was so dramatic that whether there was one or 72 galls per branch, inflorescence, pod and seed production were equally reduced. This suggested that the

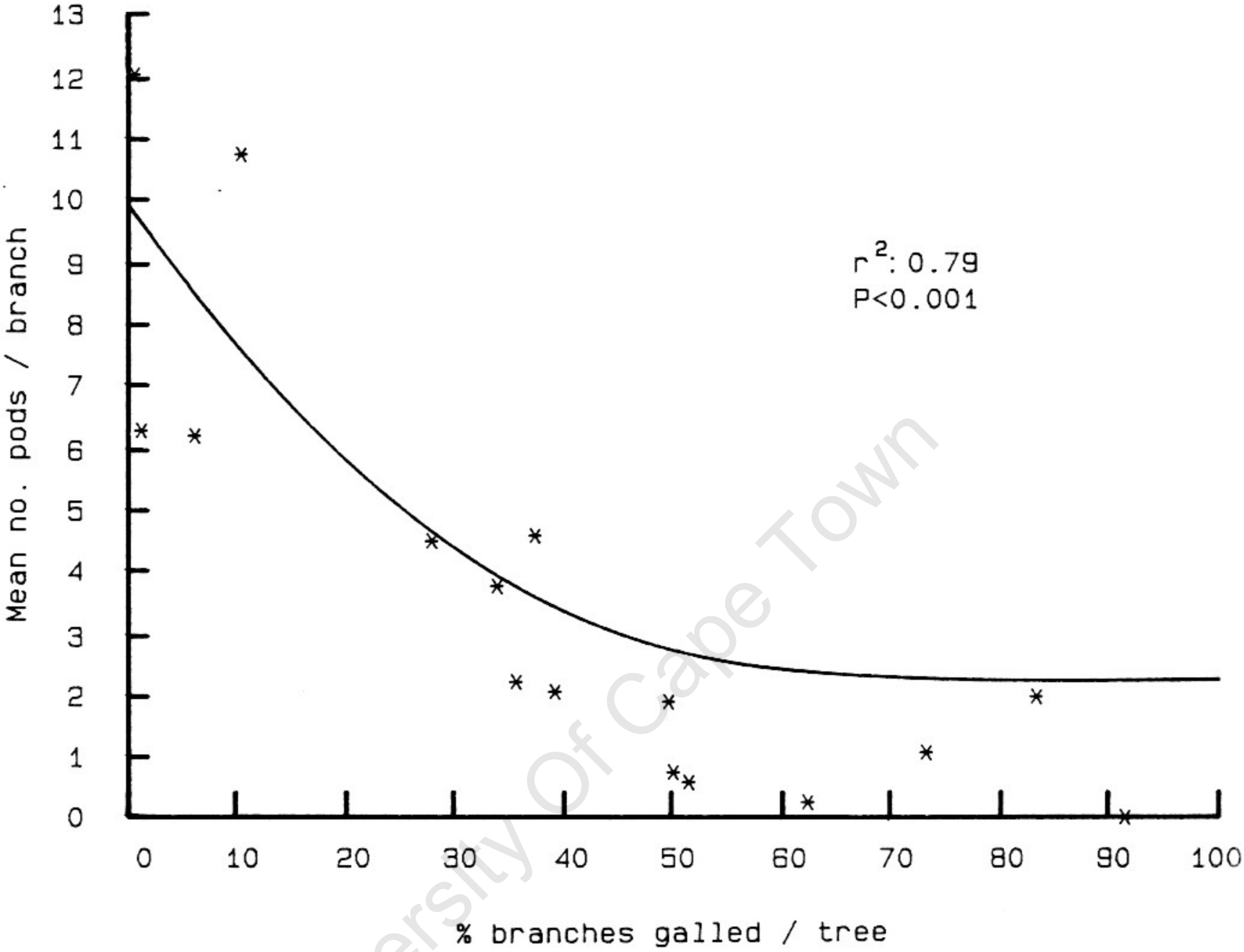


Fig. 13. The effect of varying intensities of galling by *T. acaciaelongifoliae* on pod production of *A. longifolia* trees at Vergelegen in 1983. Regression equation : $y = 9.828 + (-0.243)x + (0.002)x^2$.

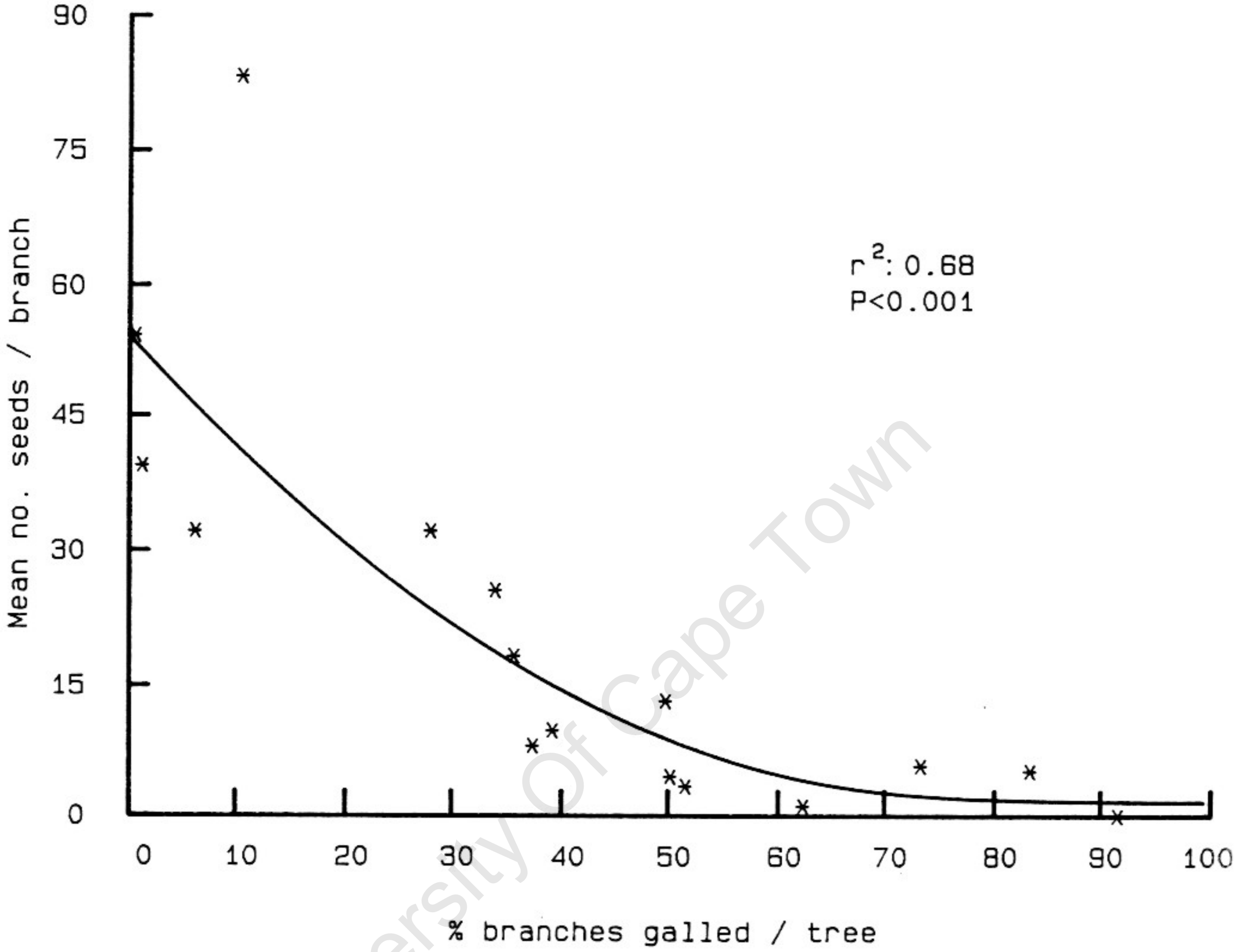


Fig. 14. The effect of varying intensities of galling by *T. acaciaelongifoliae* on seed production of *A. longifolia* trees at Vergelegen in 1983. Regression equation : $y = 53.268 + (-1.281)x + (0.008)x^2$.

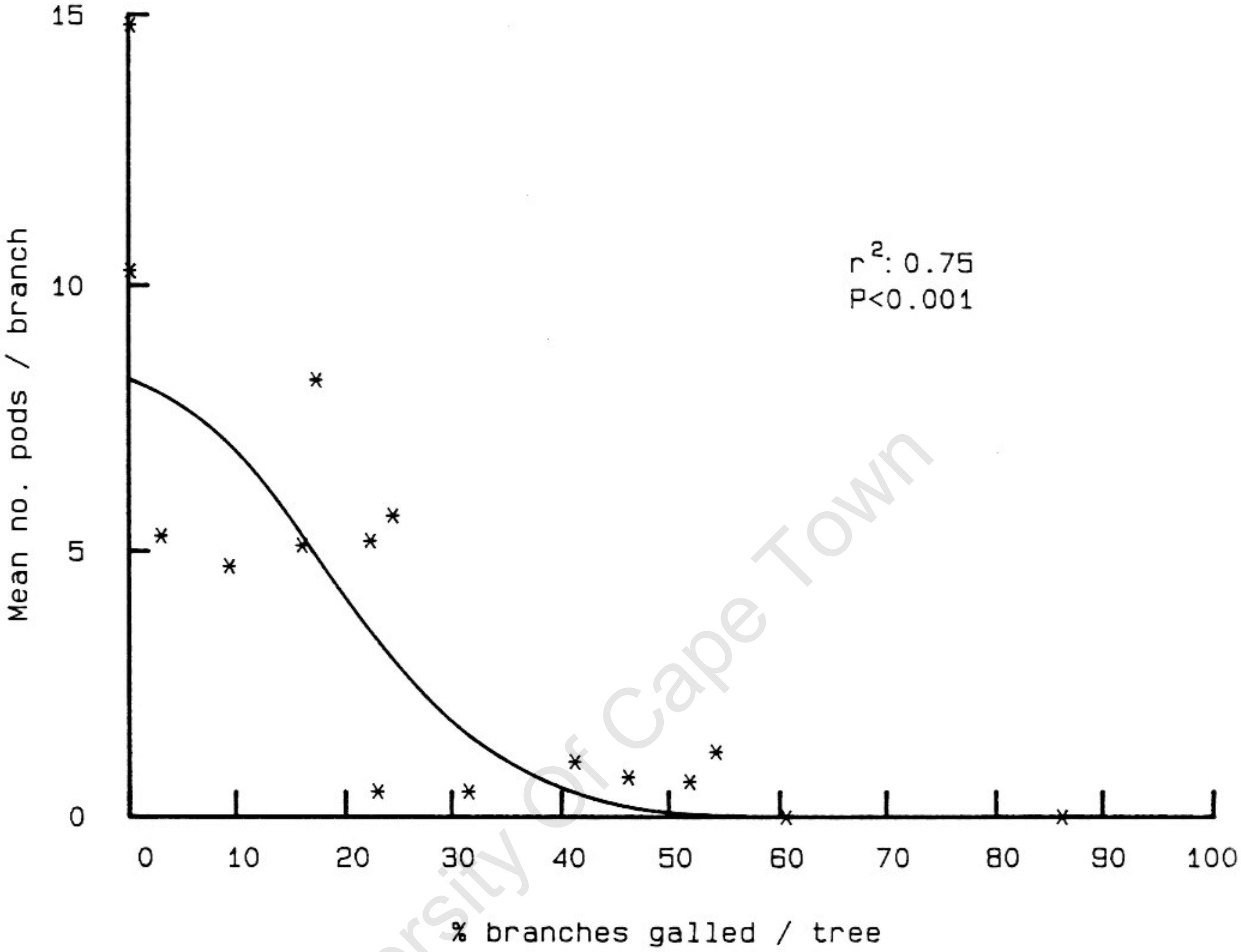


Fig. 15. The effect of varying intensities of galling by *T. acaciaelongifoliae* on pod production of *A. longifolia* trees at Eerste River in 1984. Regression equation : $y = 8.149e^{(-0.002x^2)}$.

proportion of galled branches per tree would be a good measure of the effect of the wasp on pod and seed production. The correlation between the percentage of galled branches and decreased pod and seed production of whole trees confirms both the efficiency of the wasp and the method used to demonstrate this.

The relationships between the percentage of galled branches and seed production per tree at both Vergelegen, a non-riverine site, and Eerste River, were non-linear and equally impressive. At Vergelegen the pod production of trees with over 50% of their branches galled was reduced by 89%. At Eerste River, trees with only 40% of their branches galled also suffered an 89% reduction in pod production. It was thought that the large *A. longifolia* trees with a perennial water source at Eerste River may be able to compensate to some degree for the effects of galling, but this was not the case.

***Acacia longifolia* is clearly unable to compensate for the effects of galling by *T. acaciaelongifoliae.* This is demonstrated by the non-linearity of the relationship between galling intensity and pod production. Low galling intensities thus cause relatively large reductions in seed production, indicating that the effects of galling are spread throughout the entire tree. This happens because galling reduces pod production indirectly, by enhancing inflorescence abscission, *in addition to* the direct prevention of pod development by the galling of reproductive buds. The wasp diverts so much of the plants' resources into gall production (this will be discussed in detail in Chapter 4), that the' development of ungalled inflorescences on both affected and unaffected branches on galled trees is also forfeited. The enhanced abscission of unaffected inflorescences is apparently an attempt to minimise energy output in plants stressed by galling. The gall flies *Urophora affinis* Frfld. and *U. quadrifasciata* (Meig.), which gall developing flowers in the flower heads of the knapweeds *Centaurea diffusa* Lam. and C. *maculosa* Lam., similarly reduce seed production of both affected and unaffected flower heads of galled plants (Harris, 1980b). Weis and Kapelinski (1984) have shown that the gall-midge *Rhabdophaga strobiloides* (O.S.) draws photosynthate from ungalled parts of its host, a willow plant.**

The stress caused by *T. acaciaelongifoliae* is also manifested in the suppression of vegetative growth in galled *A. longifolia* trees. The loss of phyllodes on galled *A. longifolia* branches from September to December is due to galling enhancing shoot dieback and abscission of phyllodes on the original 30-cm branch segments. By December 1983, galled branches had 53% fewer phyllodes per branch than branches on ungalled trees. After wasp emergence in mid-summer, the galls desiccated rapidly in the hot, dry mediterranean conditions, and their direct effects on the plant were terminated. The galled plants then began to recover, phyllodes being added by delayed

lateral branching only, since growth tip mortality on galled branches was 100% by mid-summer. However, the stress exerted by gall development during the first half of summer was so severe that the loss of vigour of galled plants was still significant eight months after gall desiccation when the reduction in both number of phyllodes and dry mass of galled branches was approximately 30%. In comparison, the gall flies *U. affinis* and *U. quadrifasciata* caused a 71% reduction in dry mass of diffuse knapweed *C. diffusa* (Harris, 1980b), and the stem gallers, *Eurosta solidaginis* (Tephritidae) and *Gnorimoshima gallaesolidaginis* (Gelechiidae), caused significant reductions in leaf biomass and shoot production of *Solidago canadensis* L. (Hartnett & Abrahamson, 1979).

Apart from the draining effect of galling, the inability of *A. longifolia* to compensate for the effects of galling is partly explained by the loss of phyllodes and the suppression of vegetative growth of galled branches. A plant with substantially reduced photosynthetic abilities will be less able to recover. The loss of leaves is thus both a symptom of stress and a potential cause of more stress.

***Trichilogaster acaciaelongifoliae* is able to impose the indirect effects on reproduction and growth of *A. longifolia* for at least three reasons. Firstly, the wasp attacks the seed producing structures while the latter are in physiological contact with the adult plant, as opposed to seed-reducing insects which feed on seeds which are to varying degrees separated from the adult plant. Secondly, the gall wasp affects the seed producing organs throughout their entire period of development. Insects developing in the more mature pods or fruits and seeds, even while these are attached to the adult plants, are not likely to act as stress factors *sensu* Harris (1981) on the adult plants. Lastly, there is the nature of galling itself. Mani (1964) defines galls as pathologically developed cells, tissues or organs of plants that have arisen mostly by hypertrophy (cell proliferation) and hyperplasy (abnormally large cell size) under the influence of parasitic organisms. Galling benefits the gall maker and the plant undergoes various injuries including re-directions of growth and sap flow. Flower- or seed-attacking insects that simply destroy seeds or seed producing structures without any accompanying physiological and physical distortions are unable to exert additional stress on the adult plant.**

For example, the hakea fruit moth *Carposina autologa* Meyr., that was introduced from Australia to reduce seed production of silky hakea *Hakea sericea* Schrader in South Africa, attacks mature seeds when they are completely separated from the parent plant (Annecke & Neser, 1977; Neser, 1968). The weevil *Erytenna consputa* Pascoe, also released to reduce the seed production of silky hakea, attacks, sterilises and deforms 4-week-old fruits (Kluge, 1983). The fruiting organs of the hakea are thus attacked by

these insects at a much later stage than those of *A. longifolia* are attacked by the gall wasp, and no accompanying stress is exerted on the parent hakea trees.

The gall wasp *T. acaciaelongifoliae* is able to maintain on a large scale the levels of infestation found on individual trees during the present part of this study (Chapter 1; Dennill, 1987 in press; Appendix 2). The 95 to 99% seed reduction that occurs on many trees may be insufficient to stop the the weed's dispersal and to reduce the density of the expanding weed population. Harper (1977) cites examples of such failure. However, a 95 to 99% seed reduction should markedly reduce the rate of spread of any plant (Harper, 1977). The effect of animals, especially birds, which disseminate *A. longifolia* seeds, is unknown at present and will affect the rate of spread of the partially controlled weed. Despite these reservations, if the wasp is able to achieve these levels of seed reduction wherever it is released, it will have fulfilled the purpose for which it was introduced. *T. acaciaelongifoliae* can also be regarded as a success by Harris'(1981) criterion which suggests that a successful biological control agent is one that is able to measurably increase the stress load on the target weed. Before examining the reasons why *T.acaciaelongifoliae* is able to have such devastating effects on *A. longifolia,* some salient aspects of the phenology of *A. longifolia* first need to be explained in the next chapter.

CHAPTER 3

The importance of understanding host plant phenology in the biological control of *Acacia longifolia*

ABSTRACT

In order to assess the effect of the introduced gall wasp on *A. longifolia,* it was necessary to study the vegetative growth and reproductive potential of ungalled trees. The growth of branches on ungalled trees was studied over one year. The results yielded a growth phenology which is notably different from the growth phenology of *A. longifolia* described by Milton (1980). Milton (1980) observed no distinct flushing, but a gradual increase and decline in growth during spring and late summer, repectively. The present study showed distinct flushing, and a marked lack of growth during spring. Examination of the effect of reproduction on the vegetative growth of *A. longifolia* explains the disparity. *Acacia longifolia* reproduces during spring. Comparison of phyllode addition during spring with pod production for three successive years at one site, and for two years at another, shows that phyllode addition is low during years of high pod production, and *vice versa.* Between trees, phyllode addition is also inversely related to pod production within a reproductive season. Because the present growth phenology study was done during a year of high pod production, growth during spring was negligible, in contrast to Milton's (1980) study which was done in a year of low pod production and high phyllode addition. Unless these factors are taken into account, the researcher conducting an experiment in a particular year could under- or overestimate the reproductive potential or vegetative growth of this weed by as much as 62% or 90%, respectively. This study shows that the phenology of weeds with an annual cycle needs to be examined for at least two years in order to gain a more accurate estimate of their reproductive or growth potential, and that this is especially important when assessing the efficacy of biological control agents.

It has been shown that in addition to reducing seed production, *T. acaciaelongifoliae* also reduces vegetative growth of *A. longifolia* (Chapter 2; Dennill, 1985; Appendix 1). In order to demonstrate these effects, the reproductive potential and vegetative growth of ungalled trees needed to be studied as controls. The data presented here were obtained for that purpose, and consist of *(a)* a study of the growth phenology of *A. longifolia* over a one year period, which led to (b) an examination of the effect of reproduction on vegetative growth of *A. longifolia* both in successive seasons (over a three and two year period at two study sites, respectively) and within a particular season. This information has been accepted for publication (Dennill 1988a in press; Appendix 3).

METHODS AND RESULTS

Growth phenology

In September 1983, 60 branches were randomly selected on 31 *A. longifolia* trees at Vergelegen. Of the 60 branches, 20 were selected at each of three heights, 1.0, 1.5 and 2.0 m. From September 1983 until August 1984, monthly counts were made of the phyllodes on the original 30-cm segment, the phyllodes added by apical growth of the 30-cm shoots, and phyllodes added by lateral branching. The number of phyllodes was totalled to provide a monthly index of growth throughout the study period.

Vegetative growth displayed marked flushing ; three periods of active phyllode addition were noted during December, April and July (Fig. 16). During the periods between these flushes, namely late summer and winter, phyllode addition practically ceased. It is particularly noteworthy that growth was also negligible during early summer from September (spring) until December 1983.

Effect of reproduction on vegetative growth

At Vergelegen in 1984 and 1985, 40 and 150 branches were selected on 10 and 30 trees, respectively, in the manner described above. At Banhoek River in 1984 and 1985, 60 and 33 branches were similarly selected on 22 and 20 trees, respectively. For all of these branches, and those selected at Vergelegen in 1983 (see section above), final pod production per branch and the number of phyllodes added during the reproductive period from September to mid-November (when the seeds are dropped), were determined. Independent sets of sample trees were selected randomly each year. All of the trees used were, however, within an area of 100 by 100 m.

The 40 branches marked at Vergeglegen in 1984 were selected in such a way that four branches were on each of 10 *A. longifolia* trees. In order to determine the relationship between vegetative growth and pod production within a reproductive season, the number of phyllodes added to each branch over the reproductive period (from September to mid-November) and the number of pods produced per branch were averaged for the branches from each tree.

The annual pod production of *A. longifolia* trees at Vergelegen and Banhoek varied markedly between years (Figs. 17 & 18). The results indicate that pod production is cyclical, years of high pod production being followed by years of lower pod production,

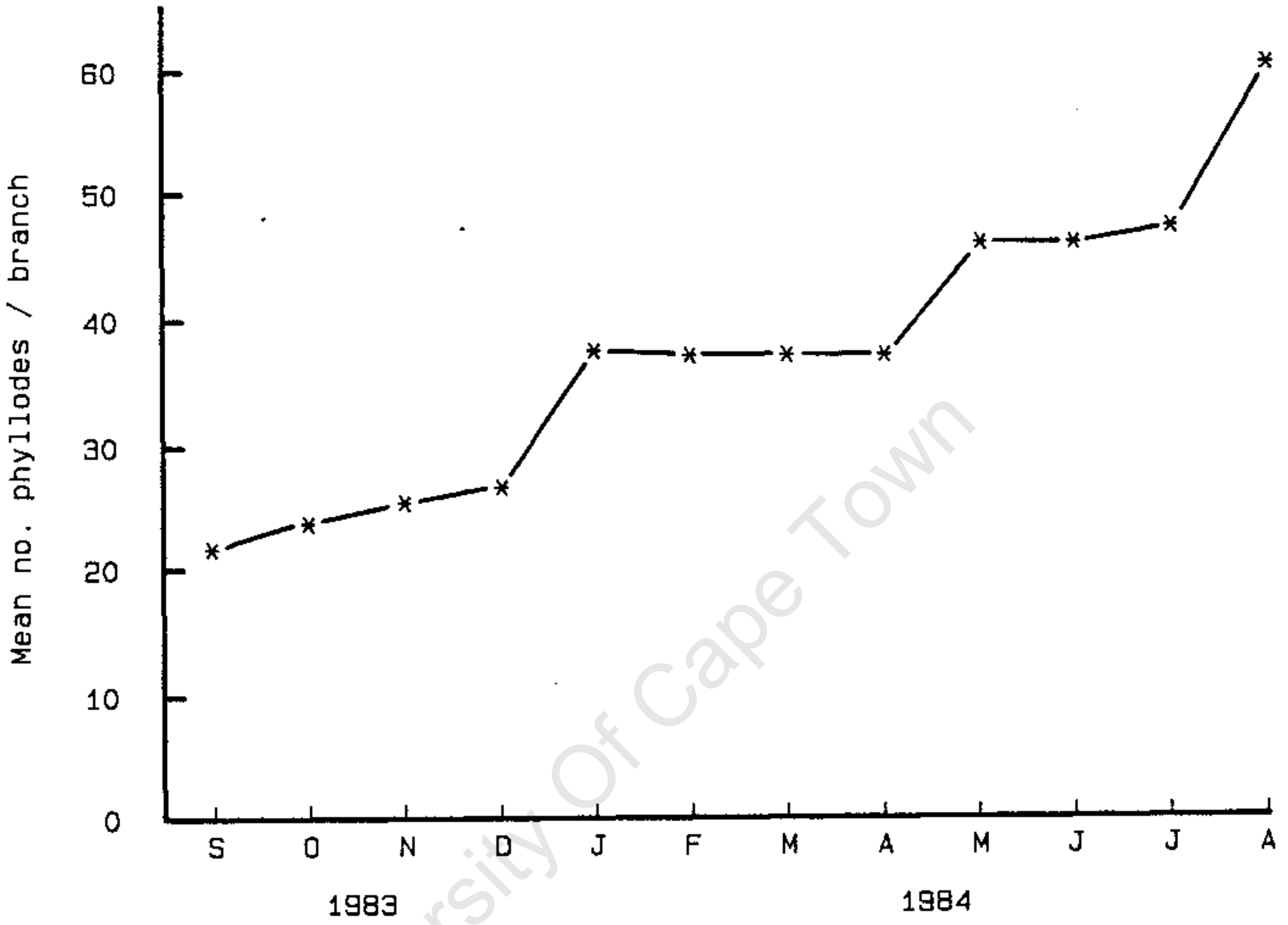


Fig. 16 The growth phenology of *A. longifolia* from September 1983 until August 1984 at Vergelegen.

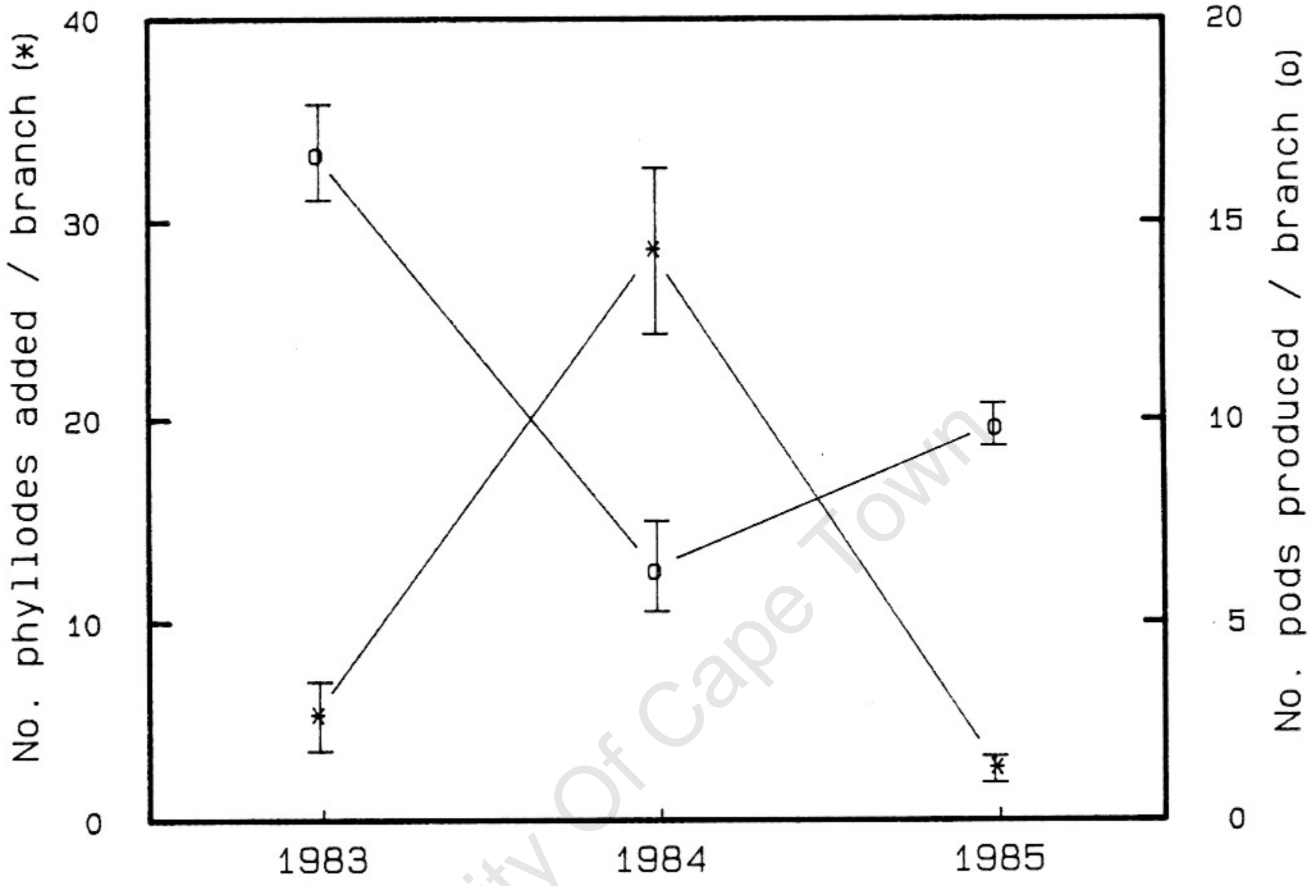


Fig. 17. Pod production (o) in relation to phyllode addition during reproduction (*) for *A. longifolia* trees at Vergelegen in 1983, 1984 and 1985. The bars at each data point represent the confidence limits (P = 0.05) of the means.

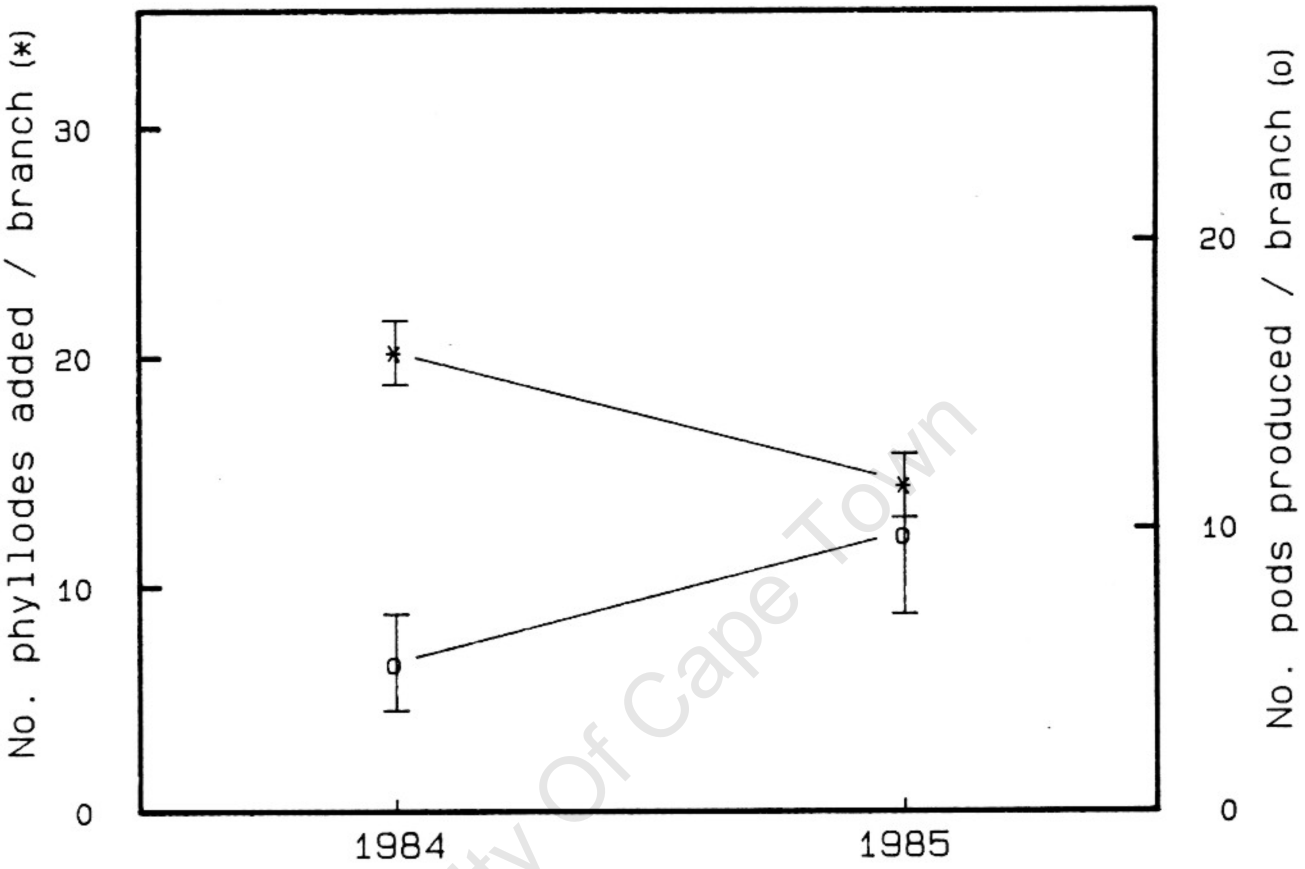


Fig. 18. Pod production (o) in relation to phyllode addition during reproduction (*) for *A. longifolia* trees at Banhoek River in 1984 and 1985. The bars at each data point represent the confidence limits (P = 0.05) of the means.

and *vice versa.* More important, however, is the fact that vegetative growth during spring was markedly reduced during years of higher pod production. This effect was more evident at Vergelegen, a drier non-riverine site than the site at Banhoek River where the trees have a perennial water source.

At Vergelegen, the number of phyllodes added during the reproductive phase was strongly negatively correlated with the number of pods produced per branch during early summer in 1984 (Fig. 19), a year of low pod production at this site (Fig. 17).

DISCUSSION

The growth phenology of *A. longifolia* from January to August is relatively easy to explain in terms of climate. *Acacia longifolia* originates from an area of all year rainfall in south-eastern Australia (Costermans, 1981). The cessation of vegetative growth from January to March is thus probably due to the fact that these are the hottest and driest months of the year in the south-western Cape Province. The growth flush observed during April was probably due to the onset of the rainy season coupled with mild temperatures. During May and June, growth again ceased because of low temperatures and short daylength. By the beginning of August, increasing temperatures and daylength, and the availability of rain can explain the growth observed here. Milton (1980) also recorded (a) a secondary growth phase in autumn, (b) minimal growth during winter when monthly temperatures fell below 15 C and daylength below 7.5 sunlight hours per day and (c) the initiation of growth during late winter.

The growth phenology observed in this study from September 1983 until January 1984 is, however, unrelated to climate ; temperatures are equable, and water availability is high at the end of the rainy season which would have replenished soil-borne water sources. Yet growth was minimal from September until November. In contrast, Milton (1980) recorded the largest growth increments during this period, and that the increment was gradual and steady during early summer (Fig. 20). She emphasised that the increase and subsequent decline in growth of *A. longifolia* during early and late summer, respectively, was gradual and unlike the other alien Australian *acacias e.g. A. melanoxylon* which displayed distinct flushing. Why, in the present study was there so little growth during this period from September to November, followed by a distinct flush during December? My thesis is that I studied the growth phenology of this species during a year of high pod production whereas Milton (1980) studied it during a year of low pod production.

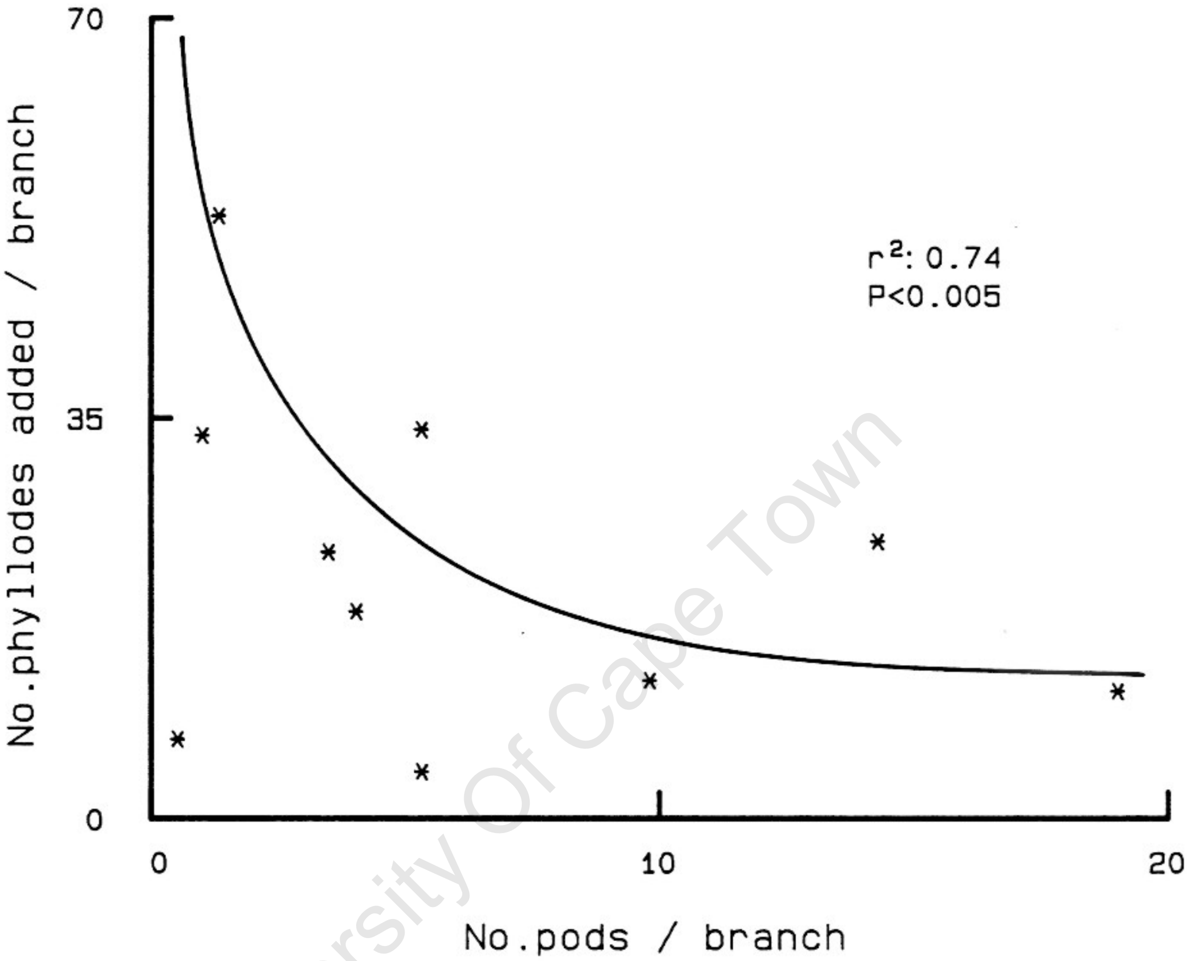


Fig. 19. The effect of pod production on spring vegetative growth of *A. longifolia* trees at Vergelegen in 1984. Regression equation : $y = 14.448 + 28.444/x$.

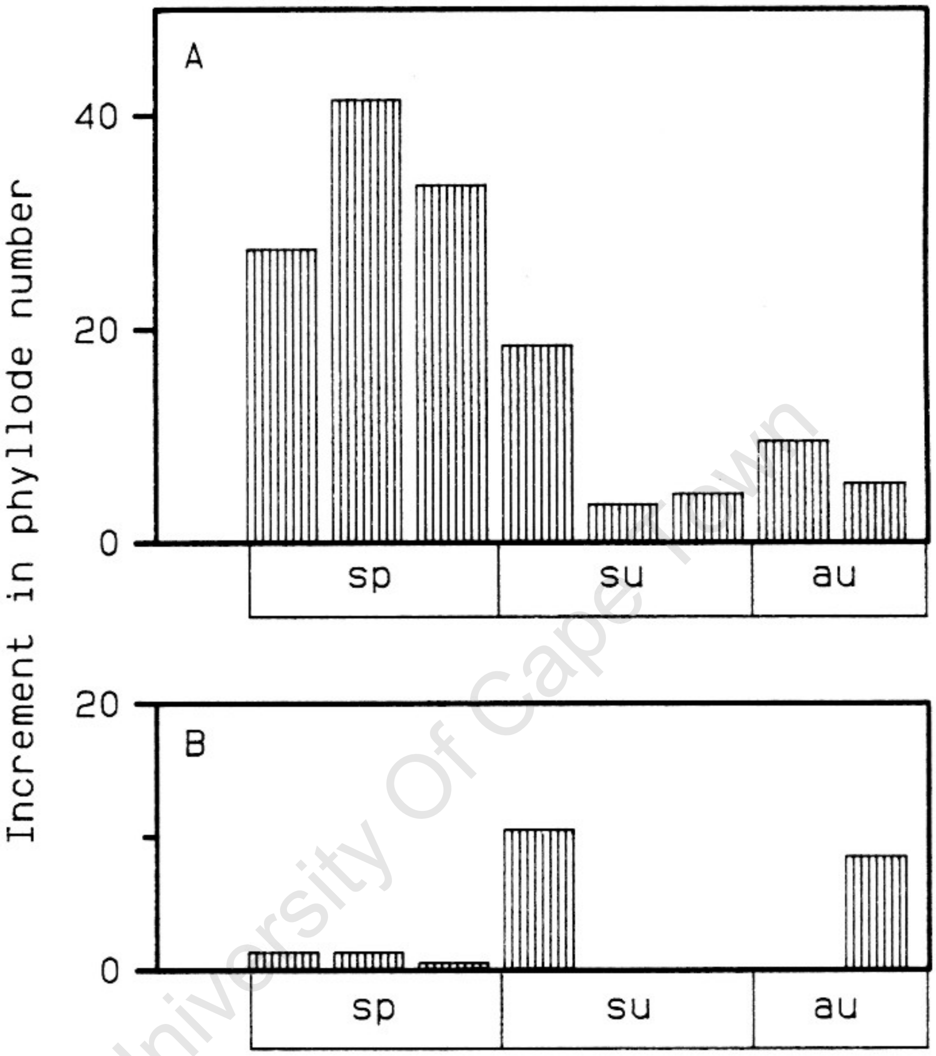


Fig. 20. The growth phenology of *A. longifolia* according to Milton (A) (reproduced from Milton (1980)), and a directly comparable phenology based on the data collected in the present study (B). sp = spring, su = summer, au = autumn.

The present study shows clearly that pod production of *A. longifolia* is inversely related to vegetative growth, both within a reproductive season, and between successive seasons. The cost of pod production to *A. longifolia is* so great that even during 1984, a year of low pod production at Vergelegen, the number of phyllodes added during the reproductive phase was strongly inversely related to the number of pods produced per branch. In a year when pod production is high, these pods are produced at the expense of vegetative growth. Nineteen-eighty-three was a year of high pod production at Vergelegen (Figure 17). This explains why no growth occurred between September and November in 1983 at Vergelegen (Figure 16). After pod maturation and seed drop had occurred in November, a growth flush occurred in December before summer temperatures became too high and water availability too low.

There is also evidence from Milton (1980) to support this hypothesis. I quote from Milton on the fruiting success of *A. longifolia* during the same year at the site at which her growth phenology was done: "Although *A. longifolia* generally sets abundant fruit at the University site, yields appear to be chronically low on certain individuals [and on parts of the tree that receive little sun]" (page C15). Regarding another Australian acacia species studied, Milton similarly notes that "The observed poor crop on *A. podalyriifolia* [A. Cunn ex G.Don.] may be due either to environmental factors *or an inherited trait"* (page C15) (my italics). It appears that these alien acacias do indeed have inherent mechanisms determining the allocation of resources between growth and reproduction and that these may be expressed cyclically, subject to prevailing climatic and edaphic factors. Morris (1951) found that balsam fir usually set heavy crops of flowers and seeds every second year, and that the quantity of foliage (number of needles) produced during flowering years was much less than in non-flowering years. He specifically mentions that the number of needles is determined by the number of primordia produced during the previous season. This suggests that the resources for growth or reproduction are determined in advance. Li (1984) has shown that removing the flower buds of *Paulownia* trees could prevent the consumption of large amounts of nutrients for reproduction and hence increase their volume compared with untreated trees.

The ability of the gall wasp *T. acaciaelongifoliae* to reduce pod production of *A. longifolia* was first studied at Vergelegen in 1983 (Chapter 2; Dennill, 1985; Appendix 1). Galled branches averaged 0.2 pods as opposed to 16.7 on branches from ungalled trees. If that study had been done at the same site in 1984, when pod production of ungalled trees was lower (6.3 pods/branch), the reduction in pod production due to the wasp would not have been numerically as impressive, and the reproductive and growth

potential of the weed could have been under- or overestimated by 62% or 90%, respectively.

These studies indicate that caution must be taken not to base phenologies of plants with annual cycles on one year's data. In particular, the biological control researcher must not assess the reproductive or growth potential of such a weed after only one year of study. In the case of understanding the efficacy of *T. acaciaelongifoliae* (which was demonstrated in Chapter 2), the knowledge that reproduction in *A. longifolia* is such an energy expensive process is of paramount importance, since it will be shown in the the next chapter (Chapter 4) that the galling caused by this insect coincides with the plant's reproductive phase and diverts far more energy than the normal reproduction of the plant.

CHAPTER 4

Aspects of the interaction between *Trichilogaster acaciaelongifoliae* and *Acacia longifolia* which account for the success achieved with this agent

ABSTRACT

The present chapter explains how the wasp is able to exploit its host plant so effectively under South African conditions where it is not limited by parasites and predators:

a. The dry mass of developing galls was significantly greater than that of the corresponding reproductive organs throughout the reproductive season of the host plant, peaking in spring (September) when galls were 25 times the mass of unfertilised inflorescences. The energy content (kj/g dry mass) of developing galls was consistently only 7% lower than that of the reproductive structures, indicating that the energy diversion to gall production was only 7% lower than the biomass diversion to gall production.

b. The dry mass of multiple-chambered galls was significantly greater than that of pods, whereas the dry mass of single galls did not differ from that of pods. The large biomass diverted to gall production is thus accounted for by a high proportion (66-73%) of multiple-chambered galls.

c. The extent of biomass diversion to gall production was relatively greater during the earlier part of the reproductive season, a factor enhancing stress on the host.

d. The wasp sometimes forced the plant to produce up to 200% more galls per branch than the normal quota of inflorescences produced by the plant. This phenomenon, called forced commitment, further increases stress on the host plant.

e. Galls constituted up to 21% and 40% of the dry and wet biomass of above-ground parts of galled trees, respectively. This caused breakage and mortality of large branches and stems.

f. Reproduction in *A. longifolia* has been shown in Chapter 3 to be so energy consuming that vegetative growth is strongly inversely related to pod production. Because the stress from galling by *T. acaciaelongifoliae* coincides with and replaces reproduction with a greater stress, successful reduction of both reproduction and vegetative growth are achieved.

Galling by *T. acaciaelongifoliae* was shown in Chapter 2 to have dramatic effects on both the reproduction and growth of galled *A. longifolia* trees. Seed production of galled trees was inversely and non-linearly related to the proportion of galled branches per tree. Pod production of trees with >50% of their branches galled was reduced by 89% to >95% at two sites, irrespective of tree size. The vegetative growth_ of galled plants was also substantially reduced. The non-linearity of the relationship between galling intensity and pod production was the result of galling enhancing the abscission of unaffected inflorescences on galled trees. This enhanced inflorescence (and phyllode) abscission is the key to this insect's ability to exploit its host in the absence of parasitism and predation. The aim of the present chapter is to explain how this is achieved. The

timing, duration and extent of biomass diversion caused by the gall wasp are examined. These factors are related to the phenology and energy allocations of the plant, which have been discussed in Chapter 4. The emphasis of the present chapter is thus on those aspects of the *interaction* between the gall wasp and its host plant that account for the success obtained with *T. acaciaelongifoliae.* The attributes of the wasp which have contributed to its ecological success (success of establishment) have already been dealt with in Chapter 1. The data from the present chapter will be reported in Dennill (1988b in press) (Appendix 4).

METHODS AND RESULTS

Energy sink and coincidence of galling with host plant reproduction

At monthly intervals from July to November 1984, 10 galled branches (with one or more galls/branch) were selected from each of 10 randomly chosen galled trees at Vergelegen. The branches were sampled in equivalent numbers at each of three heights, 1.0, 1.5 & 2.0 m on the trees which displayed a range of galling intensities from 5 to 95% galled branches per tree. Ten branches were similarly selected from 10 ungalled trees every month. The developing galls and the reproductive structures were removed from the galled and ungalled branches, respectively. The dry weights of the galls and the inflorescences were determined after drying them at 60 C for three days. Because the developing inflorescences were light, the mean weight for all the inflorescences on each of the 100 ungalled branches was determined. The number of replicates for each mean weight was therefore at least 100. The number of galls used to obtain an average dry weight per gall for each month varied from 97 to 145 (mean 119).

The monthly samples of developing galls and inflorescences collected from July until November 1984 at Vergelegen were then milled, and their energy content determined (kj/g dry mass) using an Auto Bomb Calorimeter.

At various stages of gall development, gall dry mass was 3 to 25 times that of the developing reproductive organs of *A. longifolia* (Fig. 21). For the comparison of the energy content of developing galls and reproductive organs (Fig. 22), the regression co-efficients (for slope) did not differ significantly from each other ($P > 0.50$) or zero ($P = 0.88$ & 0.54), but the Y intercepts differed significantly ($P < 0.001$), indicating that the energy content of galls was consistently only 6.8% lower than that of the normal reproductive structures throughout their development. *Trichilogaster acaciaelongifoliae*

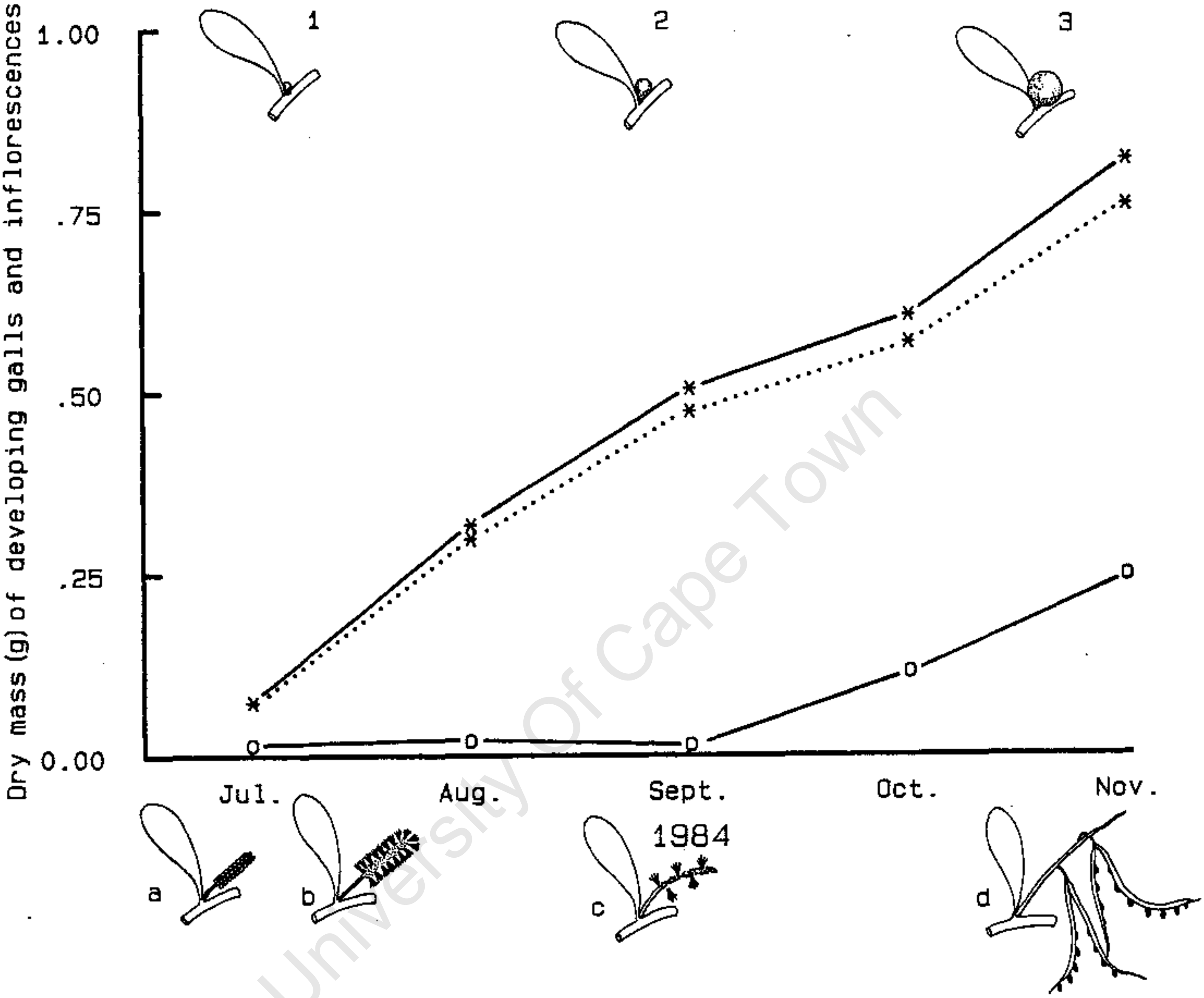


Fig. 21. Monthly comparisons of the dry mass of developing galls (*) and the reproductive organs (o) of *A. longifolia* at Vergelegen from July until November 1984. The dotted line represents nett effective gall biomass since the energy content of galls is 7% lower than that of normal reproductive tissue (see Fig. 22). 1, 2 & 3 = a gall developing to maturity in the axil between a phyllode and a branch in the place of reproductive organs ; a = an unopened inflorescence or spikelet, b = an inflorescence with opened flowers, c = a fertilised inflorescence after the unfertilised flowers have abscised, d = mature pods and seeds. Both sets of sketches are drawn to correspond with the appropriate month of the year.

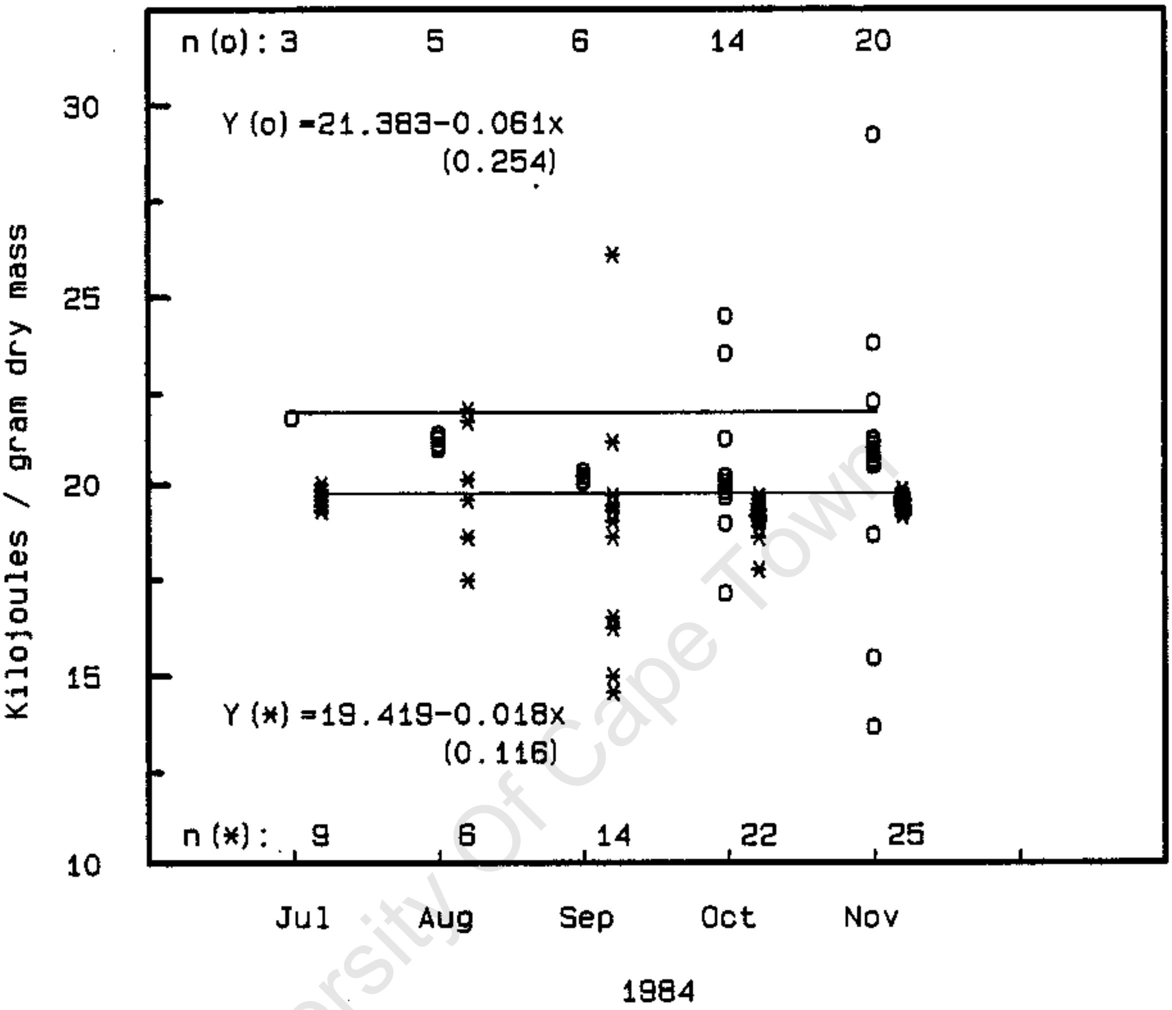


Fig. 22. The energy content (kj/g dry mass) of developing galls (*) and the reproductive organs (o) of ***A.*** *longifolia* from July to November 1984 at Vergelegen.

gall production thus consumed 3 to 23 times more energy than reproduction of *A. longifolia* at various stages of gall development (see corrected line Fig. 21).

Galling not only spanned the reproductive phase of *A. longifolia,* but energy diversion to gall production was greatest during the early part of the reproductive season from July to September when gall dry mass and energy consumption increased rapidly from 4 to 25 times and 3.9 to 23 times that of fertilised inflorescences (Fig. 21).

Effect of multiple galls

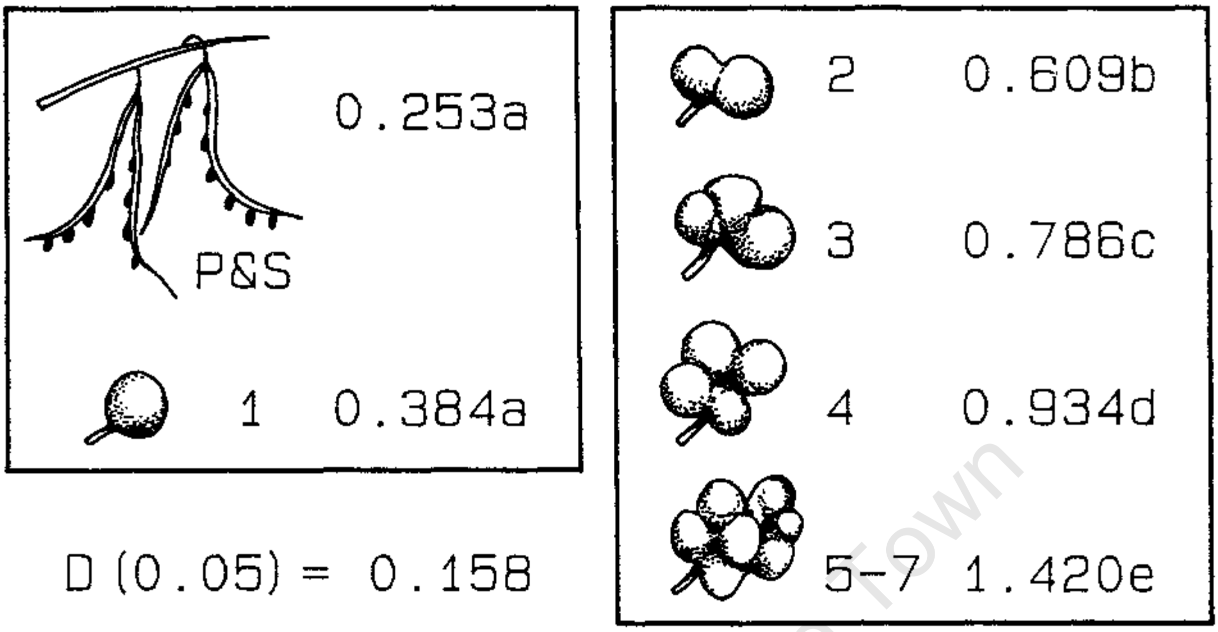
In mid-November 1984 when the pods were ripe, a large sample of galls (1033) was collected at Vergelegen from 30 trees displaying the entire range of galling intensities (1-95% galled branches/tree). Instead of comparing the mean dry weight of all the galls with that of the pods and their stalks, the galls were separated into classes according to the number of chambers per gall (Plate 4). The dry weights of the galls in these classes were compared with each other and with the dry weights of ripe pods and their stalks. The proportion of multiple-chambered galls was recorded for this sample of galls, and for another sample of 816 galls similarly picked from 30 trees at Vergelegen in 1984.

The cost of production of single-chambered galls was not greater than that of pods, but multi-chambered galls were significantly more energy consuming than both of the former (Fig. 23). The high proportion of multiple galls (73% and 66% in 1985 and 1984, respectively) thus accounts for the large amount of energy diverted to gall production.

Forced commitment

During spring (September) 1985, 200 branches with one or more galls/branch were labelled on 40 galled trees at Vergelegen, and 100 galled branches were labelled on 20 galled trees at Banhoek River *(i.e.* 5 branches/tree). Although these trees were randomly selected, all had more than 75% of their branches galled because levels of attack were high at both sites (Chapter 1; Dennill, 1987 in press; Appendix 2). As controls, 150 and 33 branches were similarly marked on 30 and 6 ungalled trees at Vergelegen and Banhoek respectively. Fewer ungalled branches were obtained than galled branches at both sites because of the scarcity of ungalled trees, especially at Banhoek River. In mid-November, the inflorescences that survived to produce pods on the ungalled branches, and the galls that matured on the galled branches, were counted. The same data had been collected for 40 and 60 pairs of galled and ungalled branches at Vergelegen and Banhoek River in 1984. The final production of galls and inflorescences

Plate 4 Mature *T. acaciaelongifoliae* galls (x0.5) picked from galled *A. longifolia* trees in November. The galls on the left are single-chambered and those on the right are muliple-chambered.



Class	n	%
P&S	102	
1	281	27 (34)
2	231	73 (66)
3	233	
4	126	
5-7	162	

Fig. 23. Comparison of the dry mass (g) of mature pods and their stalks (P & S) of *A. longifolia* with the dry mass of mature galls composed of varying numbers of chambers (1, 2, 3, 4, or 5 - 7) in November 1984 at Vergelegen. Mean dry masses followed by the same letter do not differ significantly whereas those followed by different letters do. The frequency of multiple galls is shown, and that for another sample of mature galls picked at the same site in November 1983 is given in parentheses.

per branch on galled and ungalled plants, respectively, could thus be compared for both sites in 1984 and 1985.

The wasp sometimes committed the plants to the production of up to 200% more galls per branch than the normal quota of inflorescences that the plants were able to produce (Table 12). This phenomenon, which I term *forced commitment,* **greatly increases stress on the weed.**

TABLE 12. Comparison of the number of galls and inflorescences per branch surviving to maturity on galled and ungalled *A. longifolia* **trees, respectively, at Vergelegen and Banhoek River in 1984 and 1985.**

Site	Year	Inflorescences per branch	No. galls per branch	LSD [P=0.05]
Vergelegen	1984	4.08	11.73	2.43
Vergelegen	1985	7.78	10.43	1.09
Banhoek River	1984	13.54	9.42	2.15
Banhoek River	1985	10.18	12.65	2.13

Above-ground biomass composed of galls

Five galled trees of various sizes, ranging from 186 to 1129 branches/tree, and with >75% of their branches galled (ranging from 75.2 to 89.4% branches galled/tree), were cut down at ground level at Vergelegen in November 1985. The galls were removed from each tree and both the wet and dry weights of the galls and of the remainder of each tree were obtained. Although these data were obtained from heavily galled trees, it has been shown that within three generations since release of the wasp, 84% and 73% of the trees at two sites (Vergelegen & Banhoek Mountain, respectively) were heavily galled *i.e.* **having >75% of their branches galled (Chapter 1; Dennill, 1987 in press; Appendix 2). The trees that were selected were thus representative of most of the trees at the study site.**

Galls constituted up to 40% and 21% of the wet and dry above-ground biomass of galled *A. longifolia* **trees,** respectively (Table 13).

TABLE 13. The proportion of the wet and dry above-ground biomass of galled *A. longifolia* trees composed of galls at Vergelegen in 1985.

Tree	Wet mass (kg)			Dry mass (kg)		
	Galls	Remainder of tree	%	Galls	Remainder of tree	%
1	5.96	23.93	19.94	1.44	13.73	9.49
2	7.63	12.95	36.24	1.53	7.05	17.78
3	5.26	8.04	39.55	1.23	4.64	20.95
4	1.18	3.70	24.18	0.33	2.00	14.16
5	11.86	28.04	29.70	2.46	15.09	14.02

DISCUSSION

Hartnett and Abrahamson (1979) raised the point that galling occurring early in the growth season of a plant is likely to have a greater effect on biomass allocation and reduction of vegetative growth than galling which occurs later in the season. Galling by *T. acaciaelongifoliae* spans the entire spring and summer growth period of *A. longifolia.* Moreover, the extent of galling was more pronounced during the earlier part of the season from July to September when the dry mass of galls rose rapidly from 4 to 25 times that of the normal reproductive structures.

More important than the coincidence of galling with the growth period of *A. longifolia* is the fact that galling also coincides with the reproductive period of this plant. The cost of reproduction for *A. longifolia is* so great that vegetative growth is sacrificed to increase pod production (Chapter 3). When galling coincides with, and largely replaces the already costly process of reproduction, this has profound effects on the growth of the plants.

Maiteki & Lamb (1985) have demonstrated this principle experimentally by examining the effects of feeding by the pea aphid *Acyrthosiphon pisum* (Harris) on field peas. Plants infested up until flowering *(i.e.* infested during the vegetative phase only) recovered, but feeding continuing through the flowering phase had dramatic effects which were similar to those caused to *A. longifolia* by *T. acaciaelongifoliae,* namely reduced dry matter production, enhanced abscission of flowers and pods, and reduction in pod production per plant. The effects caused by the aphids were attributed to

nutrient drainage, a similar effect to that of gall formation. Interestingly, aphid feeding commencing at pod filling caused no damage. The point that seed reducing biological control agents that attack the reproductive organs at more mature stages are likely to have less effect (on reproduction and vegetative growth) than those attacking less mature reproductive organs like *T. acaciaelongifoliae* has been elucidated by Dennill (1985) (Chapter 2; Appendix 1).

A comparison of the effects of the gall flies *Urophora affinis* and *U. quadrifasciata* on the diffuse and the spotted knapweed (Harris, 1980b) is also illuminating regarding the timing of gall development relative to the phenology of the host plant. Both gall fly species attack both of the knapweed species. A chemical exclusion trial showed that galled diffuse knapweed was 71% lighter, developed 71% fewer seed heads and had 57% fewer heads in a pre-flower stage at the end of the season than did ungalled plants. However, spotted knapweed galled in similar intensities by the same two fly species showed no significant difference in these parameters (Harris, 1980b). This striking difference in the effects of galling on the two knapweed species is attributed by Harris (1980b) to the difference in phenology between these two plant species. Vegetative growth and flower head development of spotted knapweed was completed early relative to that of the gall larvae, and were consequently little affected. In diffuse knapweed, however, vegetative growth and flower head development continues later than infestation of the plants by the gall flies. The gall larvae were consequently able to divert the resources which should have gone into growth and flower head production.

In the case of *T. acaciaelongifoliae,* gall development is initiated at the onset of inflorescence development, and the biomass and energy diverted to gall production is consequently great. The immediate response of *T. acaciaelongifoliae* to the cues initiating inflorescence development is possible because the wasp lives within the reproductive tissues of its host. Moreover, *T. acaciaelongifoliae* galls primordial tissue which is reputed to produce larger and more grotesque galls than galls formed in more differentiated tissue *e.g.* stem tissue (Ananthakrishnan, 1984). This is due to the plasticity of the former and the fact that a readily available and rapid nutrient flow towards these tissues is already established and operational at the time required by the gall former.

Multiple-gall production by *T. acaciaelongifoliae* would seem to be a wastage of eggs, since single-chambered galls stop pod production as effectively as multiple-chambered galls do. However, this 'inefficiency' of the wasp (from a biological control perspective) results in the high proportion of multiple-galls which in turn causes the relationship between galling intensity and pod production per tree to be non-linear. If

only single-chambered galls were produced, far less stress would be exerted on *A. longifolia* **trees. There would consequently be much less inflorescence (and phyllode) abscission, the reduction in pod production would be more linearly related to galling intensity, and much higher levels of galling than 50% galled branches per tree would be necessary to reduce pod production by 89-95%.**

Forced commitment is a consequence of the reproductive phenology *A. longifolia. Acacia longifolia* **produces an excess of reproductive buds during spring, which results in an excessive production of inflorescences during the subsequent spring. Many of these are abscised (Milton, 1980; Milton & Hall, 1981) and the number which mature to produce pods depends on intrinsic annual variations and prevailing climatic and edaphic conditions (Chapter 3; Dennill, 1988a in press; Appendix 3). This is characteristic of Australian acacias (Harley, 1985b) and is regarded as a strategy of higher plants to ensure reproduction (Addicot, 1982; Harley, 1985b). In the present case, the full quota of buds is available for oviposition by the wasp during the spring** *preceding* **that during which abscission of the excess inflorescences occurs. The galls cannot be abscised as the unwanted inflorescences can, and the plant can thus be committed to the production of many more galls than the number of inflorescences it was able to mature at the time. Apart from the physiological energy drainage, the high above-ground biomass composed of galls can also cause mechanical breakage of branches, especially during windy periods.**

The success obtained so far using *T. acaciaelongifoliae as* **a biocontrol agent is thus the combined result of certain features of the galling caused by the wasp and salient features of the phenology of** *A. longifolia* **(and these will be discussed in more detail in Chapter 6). Paradoxically, the host plant's means of both ensuring reproduction and conserving energy, abscission, is also its Achilles' heel.**

CHAPTER 5

The compatibility of the Australian gall wasp *T. acaciaelongifoliae* with the climates in the South African regions where it was released for the control of *A. longifolia*

ABSTRACT

The gall wasp *T. acaciaelongifoliae* was released at 136 sites throughout the distribution of the weed *A. longifolia* in the Cape Province and Natal. Each site was monitored annually to determine whether the wasp would establish and to determine its effectiveness where it had established. *Trichilogaster acaciaelongifoliae* did establish throughout the range of *A. longifolia.* In the cooler coastal regions of the south-western Cape and southern Cape, the wasp established well and levels of infestation were consistently high. However, in the hotter inland valleys and west coast of the south-western Cape Province establishment was poor and infestation levels were consistently low and declined over three years of evaluation. In Australia, *A. longifolia* occurs naturally along the coastal regions of southern Queensland, New South Wales, Victoria and eastern South Australia. However, the *T. acaciaelongifoliae* individuals released in South Africa originate only from the coastal regions of New South Wales and Victoria, and Tasmania. Climatically, these areas correspond most closely to the regions in which the wasp is successful in South Africa. The wasp cohorts released in South Africa thus appear to be ill-adapted to the hot conditions experienced in the abovementioned valleys in South Africa. Recommendations are made regarding the future control of the weed in these areas. The method whereby the insects were released in South Africa, and the methods for evaluating the degree of establishment and subsequent infestation levels at each release site, are described. Maps illustrating the weed distribution, the location of the release sites and the scores signifying the success of establishment at each site, are included.

The first *T. acaciaelongifoliae* galls that were imported to South Africa for this project arrived during the spring of 1981. From these galls, 1466 females were obtained. These wasps were divided into three approximately equal batches and were caged in gauze sleeves on *A. longifolia* branches at Banhoek, Vergelegen and Eertse River. The subsequent generation of wasps was allowed to disperse naturally at these sites. *Trichilogaster acaciaelongifoliae* was thus released only in 1982. These three sites were intended for evaluative research. Studies showed that *T. acaciaelongifoliae* established readily, dispersed well and built up to large populations (Chapter 1) and that it had strong potential for the reduction of seed set and vegetative growth of A. *longifolia* (Chapters 1, 2 and 4; Dennill, 1987 in press, 1985, & 1988b in press; Appendices 2, 1 and 4, respectively).

During 1982, a much larger consignment of *T. acaciaelongifoliae* galls from Australia yielded 14791 females for release at a wider range of sites. Populations were established with these insects in the vicinity of Stellenbosch at Stellenbosch Mountain,

The Boord, Klein Drakenstein and La Motte. These nursery sites for *T. acaciaelongifoliae* populations served as sources from which the wasp could be distributed throughout the range of *A. longifolia* in South Africa. All of the *T. acaciaelongifoliae* individuals released in South Africa were collected from the coastal regions of New South Wales and Victoria in Australia, and from Tasmania, by Neser (1985). The localities and co-ordinates of the sites from which these wasps were obtained are given in Table 14. In Australia *A. longifolia* occurs in a narrow band (<100 km wide) along the coasts of southern Queensland, New South Wales and eastern South Australia (Costermans, 1981). This distribution accounts for one of this plant's common names being 'coastal wattle'. *Trichilogaster acaciaelongifoliae* was collected from both varieties of *A. longifolia, namely A. longifolia longifolia* and *A. longifolia sophorae,* and *Acacia floribunda* (Vent.) Willd., all of which are known hosts of *T. acaciaelongifoliae* (Noble, 1940).

TABLE 14 The localities and co-ordinates of the sites at which *T. acaciaelongifoliae* was collected by Dr S. Neser in south-eastern Australia in 1981 and 1982, and the *Acacia* species or variety from which the collections were made. For *A. longifolia, I A. longifolia* var. *longifolia* and *s A. longifolia* var. *sophorae.* NSW = New South Wales, Vic = Victoria and Tas = Tasmania.

Year	Locality	State	Co-ordinates	Acacia sp./var.
1981	Mittagong	NSW	34°21'S;150°18'E	*l*
1981	Fitzroy Falls	NSW	34°40'S;150°42'E	*l*
1981	Jervis Bay	NSW	35°05'S;150°26'E	*l*
1981	Sussex Inlet	NSW	35°05'S;150°23'E	*l & s*
1982	Mittagong	NSW	34°21'S;150°18'E	*l*
1982	Fitzroy Falls	NSW	34°40'S;150°42'E	*l*
1982	Jervis Bay	NSW	35°05'S;150°26'E	*l & s*
1982	Moruya	NSW	35°55'S;150°04'E	*s*
1982	Melbourne	Vic	37°50'S;145°05'E	*l*
1982	Geelong	Vic	38°18'S;144°44'E	*l*
1982	Mordialloc	Vic	37°50'S;145°05'E	*s*
1982	Tyabb	Vic	38°32'S;145°23'E	*l*
1982	Launceston	Tas	41°25'S;147°10'E	*A. floribunda*

The aims of the study reported in this chapter were *(a)* to determine the present distribution of *A. longifolia* in the south-western and southern Cape as accurately as possible, (b) to release wasps collected at the abovementioned nursery sites throughout the South African range of the weed, (c) to determine whether the *T. acaciaelongifoliae*

established in all regions, (d) to evaluate annually the levels of infestation achieved by the wasp at each release site to determine whether there were any regions in which the wasp was less effective, and to determine, where possible, the reasons for this.

Another important objective of this study was to determine the fate of the release sites. Because a large proportion of *A. longifolia* infestations occurs along rivers which run through farmlands, and along roads, a large amount of human interference with the release sites was expected. The roadside distribution of *A. longifolia* is the result of seed dispersal in building sand and disturbance of the soil and vegetation by roadbuilding (Macdonald & Richardson, 1986). In this study, release sites were specifically not marked with signposts instructing people not to disturb the sites. This was done because human interference is an inevitable part of the ecology of the *A. longifolia* in South Africa and it was important to determine how much impact this would have on the survival of *T. acaciaelongifoliae,* given the manner in which the wasp was released.

METHODS AND RESULTS

Weed distribution

To determine the distribution of *A. longifolia* and locate suitable release sites for *T. acaciaelongifoliae,* the south-western and southern Cape Province, and Natal were surveyed in 1982, 1983 and 1984, respectively. The surveys were done during spring (September/October) when *A. longifolia is* easy to locate because of its profusion of yellow flowers which are of a lighter and brighter colour than those of its relatives *(Acacia pycnantha* Benth. and *Acacia saligna* (Labill.) Wendl.) which also flower at the same time of year. The infestations were marked on 1:50000 maps. Additional records were obtained from reports compiled by the members of the Weed Research Unit at Stellenbosch under the guidance of Mr. P.J. Pieterse.

The distribution of *A. longifolia in* the regions surveyed is illustrated in Figs. 24 & 25. It is not claimed that these are exhaustive records of this plant's South African distribution.

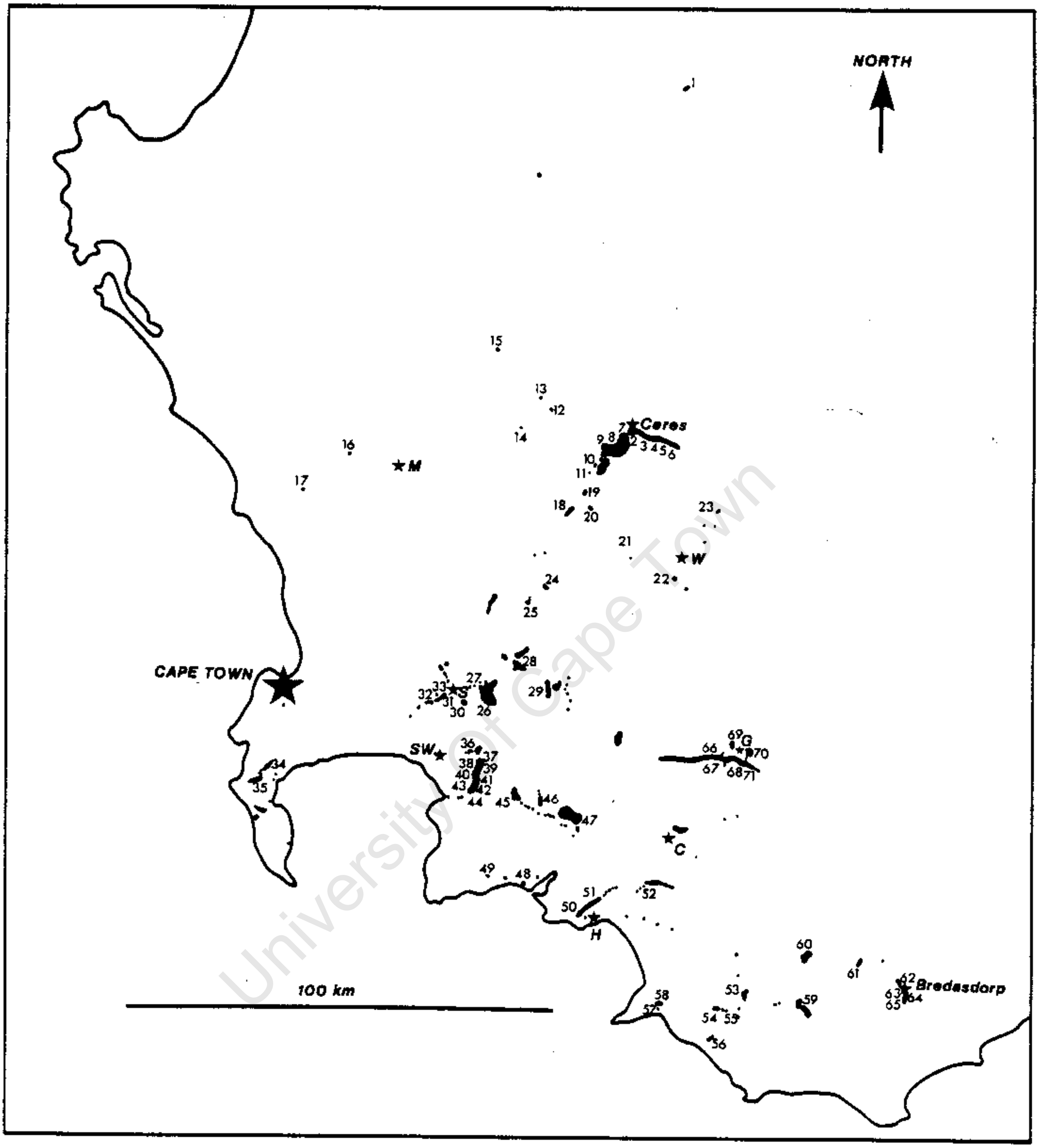
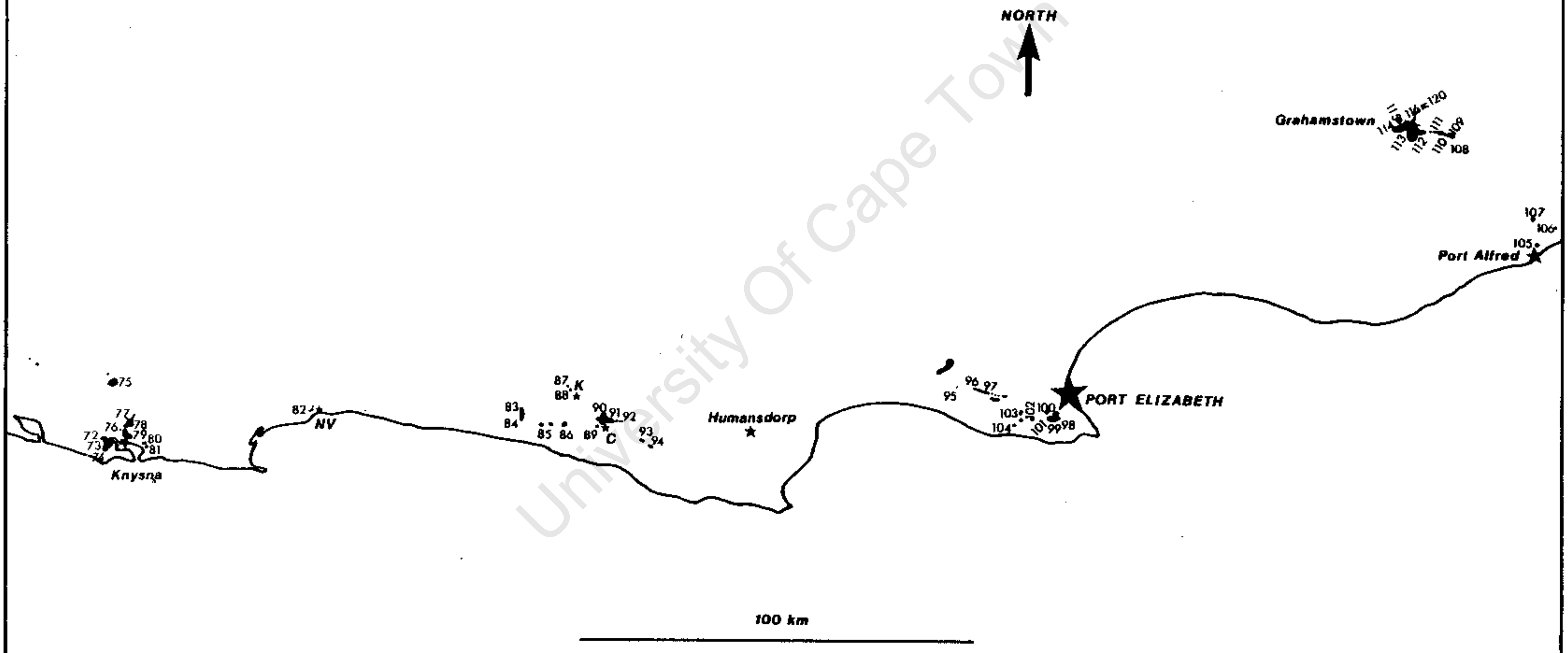


Fig. 24. The distribution of *A. longifolia* in the south-western Cape Province and the location of the sites (numbered) where *T. acaciaelongifoliae* was released in 1983. More detailed descriptions and co-ordinates for each site are given in Table 19. The stars represent cities and towns : from north to south M = Malmesbury, W = Worcester, S = Stellenbosch, G = Greyton, SW = Somerset West, C = Caledon and H = Hermanus.

Fig. 25. The distribution of *A. longifolia* in the southern Cape Province and the location of the sites (numbered) where *T. acaciaelongifoliae* was released in 1984. More detailed descriptions and co-ordinates for each site are given in Table 19. The stars represent cities and towns : from west to east NV = Nature's Valley, K = Kareedouw and C = Clarkson.



Release method and dissemination of T. acaciaelongifoliae *throughout the South African range of* A. longifolia

Trichilogaster acaciaelongifoliae galls were harvested during October when approximately 25% of the adults had emerged. (Neser (1985) found this a suitable time for harvesting galls for exportation from Australia to South Africa.) Approximately 2.5 kg of galls were placed in boxes which were 33 cm long, 27 cm wide and 19 cm deep. The boxes were closed and a flap of 5 by 5 cm, attached at its upper end, was cut out of each end of the box. The flaps were bent upwards to. provide the windows thus created with protection from excessive sunshine and rain. At each release site two boxes of galls were placed in the shade under trees with lots of bud-bearing branches and which appeared to be under little or no stress. In boxes of these dimensions, the galls lay 4 to 5 cm deep, and remained moist for long enough to allow most of the wasps to emerge. If fewer galls were placed in the boxes, they desiccated more rapidly and hardened, preventing the adult wasps from emerging.

Using this method, *T. acaciaelongifoliae* was released at 71, 49 and 17 sites in the south-western Cape Province in 1983, southern Cape in 1984 and Natal in 1985, respectively.

The locations of the 136 sites at which *T. acaciaelongifoliae* was released are shown in Figs. 24 & 25. (For more detailed descriptions and the co-ordinates of each site see Table 19 at the end of this chapter.)

Evaluation of establishment and levels of infestation of T. acaciaelongifoliae

In the first year after release, each site was inspected to determine whether *T. acaciaelongifoliae* had established there or not, and if so, to assess the degree of establishment. These assessments were done on the trees under which the wasps had been placed *(i.e.* the release trees). The number of release trees examined varied from 1 to 10 depending on the density of the weed. In the second and third years after release, the levels of infestation were determined for areas of approximately 10 by 10 m and 100 by 100m around the release points, respectively. The areas used for these evaluations were based on the results of detailed studies of the establishment, dispersal and infestation levels of the wasp at Vergelegen and Banhoek where the wasp had established successfully (Chapter 1; Dennill, 1987 in press; Appendix 2). In order to assess establishment and levels of infestation, visual assessments of the percentage of galled branches on attacked trees were made. The reliability of visual assessments of levels of infestation of *T. acaciaelongifoliae* on *A. longifolia* trees has been demonstrated (Chapter 1; Dennill, 1987 in press; Appendix 2).

The scale whereby the degree of establishment of *T. acaciaelongifoliae* on release trees was rated for each release site one year after release is as follows: 0 = no establishment; 1 = very poor (few galls located with difficulty after searching for 0.75 hr); 2 = poor (galls easier to locate but sparse); 3 = medium (galls readily visible on release trees and approximately 50% of the branches on the release trees galled); 4 = good (approximately 75% of the branches on release trees galled); 5 = extremely good (>75% branches on release trees galled. At these levels of infestation, namely >75%, the release trees would have been sterilised (Chapters 2 & 4; Dennill, 1985 & 1988b in press; Appendices 1 & 4, respectively)).

The scale whereby the levels of infestation were determined for each site at which *T. acaciaelongifoliae* had established for the second and third years after release is as follows: 0 = population died; 1 = very low populations (<10% of the branches galled); 2 = low (10 to 30% branches galled); 3 = medium (30 to 60% branches galled); 4 = high (60 to 75% branches galled); 5 = very high populations (>75% of the trees with 75 to 100% branches galled) and 6 = exceptionally high populations with mortality of primary branches, stems or entire trees.

The ratings for the final year of evaluation (either second or third year after release) were mapped to illustrate the levels of infestation for each region. Such a map was not done for Natal since *T. acaciaelongifoliae* was established there only in 1986;

The ratings for the degree of establishment in the four South African regions identified above are given and compared in Table 15. Final scores (from 1 - 6) for the levels of infestation recorded at the release sites in the south-western and southern Cape are recorded in Figs. 26 and 27, respectively. These results showed that *T. acaciaelongifoliae* was unsuccessful in the following regions of the south-western Cape Province: the west coast areas from Darling and Mamre in the west to Malmesbury, Porterville and Gouda in the east, and the valleys of Paarl, Worcester, Wolseley, Tulbagh, Ceres and De Dooms. In the remainder of the south-western and in the southern Cape Province, however, consistently high scores were recorded. In the southern Cape, more ratings of 'exceptionally high with mortality of primary branches, stems or trees', *(i.e.* 6's), were recorded than in either of the other regions (Figs. 26 & 27).

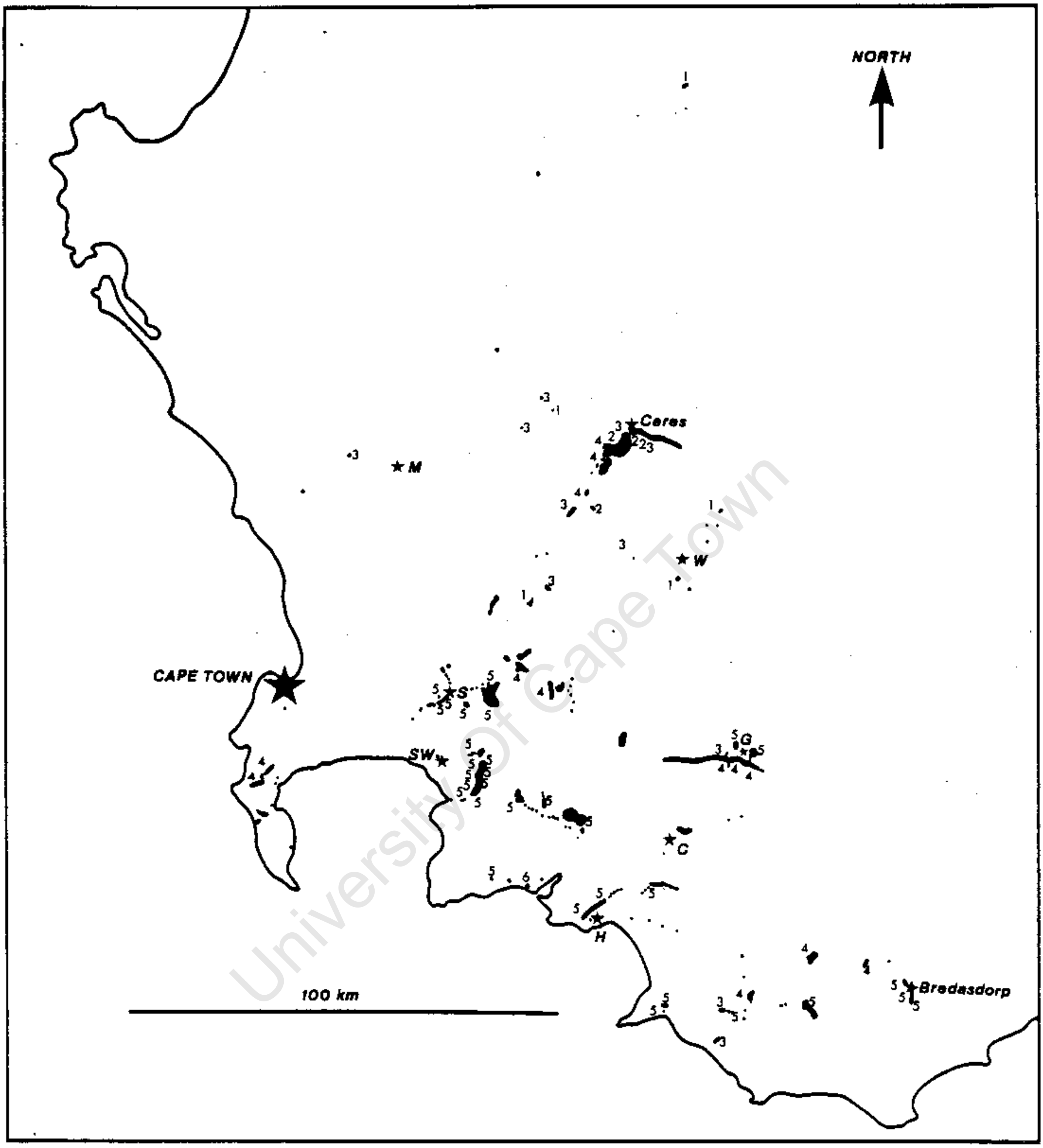


Fig. 26. The scores (1 - 6) signifying the levels of *T. acaciaelongifoliae* infestation at the release sites in the south-western Cape Province in 1986, two years after the establishment of the wasp. The stars represent cities and towns : from north to south M = Malmesbury, W = Worcester, S = Stellenbosch, G = Greyton, SW = Somerset West, C = Caledon and H = Hermanus.

Fig. 27. The scores (1 - 6) signifying the levels of *T. acaciaelongifoliae* infestation at the release sites in the southern Cape Province in 1986, one year after the establishment of the wasp. The stars represent cities and towns : from west to east NV = Nature's Valley, K = Kareedouw and C = Clarkson.

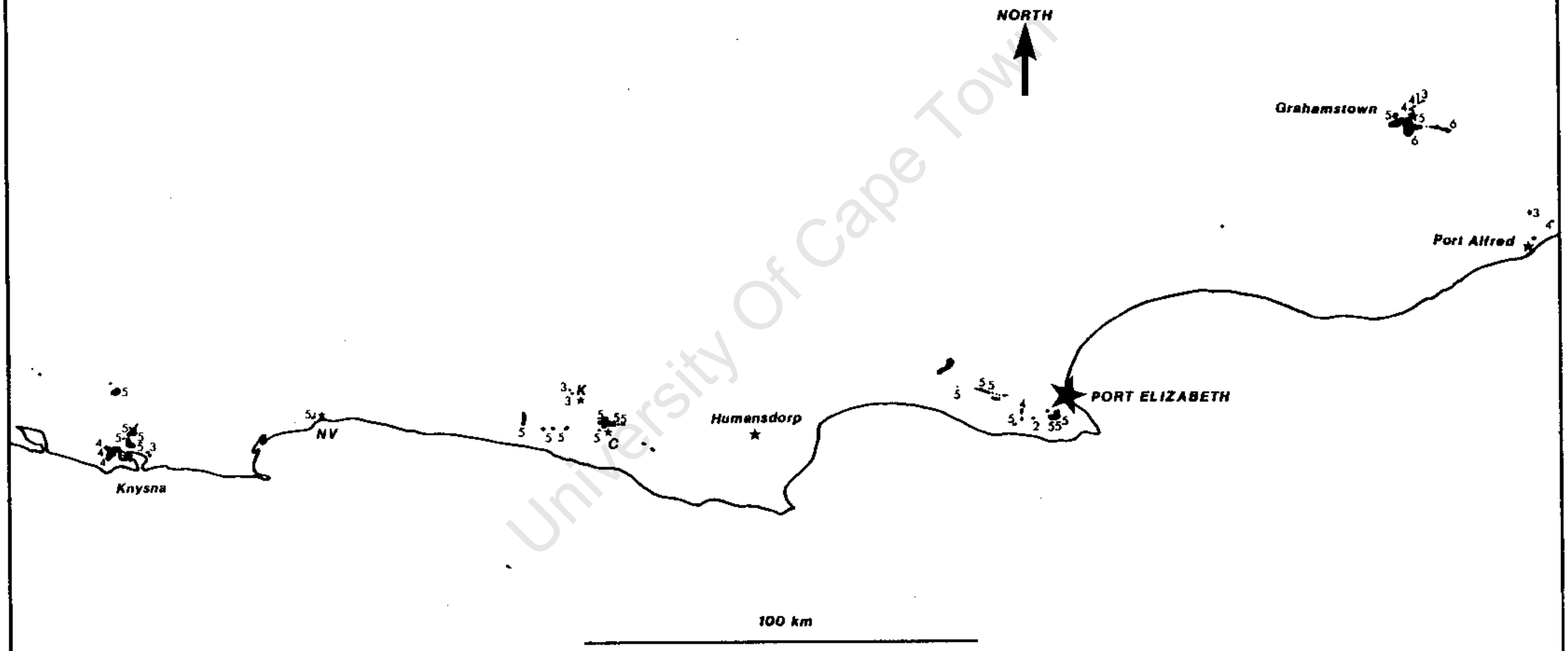


TABLE 15 Comparison of the degree of establishment of *T. acaciaelongifoliae* in (1) the inland valleys of the south-western Cape Province, (2) the coastal south-western Cape Province, (3) the southern Cape Province and (4) Natal. Avg. = average, min. = minimum, diff. = difference.

Region	n	Rank avg.	Comparison	Avg. diff.	Min. diff. (P<0.0001)
1	20	33.3	1 vs. 2	41.7	> 14.8
			1 vs. 3	24.7	> 15.1
			1 vs. 4	0.4	< 19.4
2	42	74.9	2 vs. 3	16.9	> 12.2
			2 vs. 4	42.1	> 17.3
3	38	58.0	3 vs. 4	25.1	> 17.5
4	13	32.8			

Fate of the release sites

The number of release sites which had been disturbed in any way by human activities, the type of disturbance and the number of sites at which such disturbance had resulted in the mortality of the *T. acaciaelongifoliae* population, were recorded annually.

Of the 136 release sites, only 18 sites (13%) were disturbed. The disturbance was either chopping for wood or to open watercourses, or bulldozing by roadworkers. Only 12 sites (9%) had been disturbed so severely that there was no survival of *T. acaciaelongifoliae,* and of these, only 5 had no other successful release site within 5 to 10 km. Two of these five sites were in isolated, marginal circumstances. These results show that human interference has not adversely affected the establishment of *T. acaciaelongifoliae* in South Africa.

Eco-climatic compatibility of the T. acaciaelongifoliae *cohorts released with South African climates*

The data recorded above showed that the degree of establishment and levels of infestation of *T. acaciaelongifoliae* were consistently high in the coastal south-western Cape Province and southern Cape, but consistently low in the hotter inland valleys and west coast of the south-western Cape Province. In order to compare the establishment and infestation levels of *T. acaciaelongifoliae* in the various regions, the release sites were grouped as follows:

(1) The inland valleys and west coast of the mediterranean south-western Cape Province which experience high summer temperatures. These include the Ceres, Tulbagh/Wolseley, Worcester/Hex River and Paarl Valleys, and the west coast areas of Darling, Mamre, Malmesbury, Gouda and Porterville.

(2) The mild& coastal regions of the mediterranean south-western Cape Province from Cape Town and Stellenbosch in the west to Bredasdorp and Greyton in the east.

(3) The coastal southern Cape Province from Knysna to Port Alfred and including Grahamstown. This region experiences rainfall all year.

(4) Natal, between Durban, Pietermaritzburg, Ixopo and Scottburg. This is a sub-tropical summer rainfall region.

The scores for establishment and levels of infestation of *T. acaciaelongifoliae* were compared for these regions using the Kruskal-Wallis one way analysis of variance by ranks (Siegel, 1956 pp. 184-193).

In order to determine the reason(s) for the poor results obtained in region (1), the climatic classifications of Walter & Leith (1960) and Köppen (obtained from Schulze & McGee, 1978), were superimposed on the maps showing the scores for the final evaluation of infestation of *T. acaciaelongifoliae* in South Africa (see section above). The same climate classifications for south-eastern Australia were consulted to determine to what degree the regions in which *T. acaciaelongifoliae* was successful or unsuccessful in South Africa corresponded to the regions in which the wasps had been collected in Australia. The Klimadiagrams of Walter & Leith (1960) for these regions in South Africa and Australia were also compared. In addition, the average daily maximum and minimum temperatures for each month were compared for 14, 20 and 15 weather stations in the three South African regions (regions 1, 2 & 3; data obtained from *Climate of South Africa*, 1986), and these were compared with the average daily maximum and minimum temperatures for the warmest and coldest months of the year in the Australian regions in which the wasps had been collected. Gentilli's (1971) homoclinal classification of Australia according to January maximum temperatures was also consulted. Natal was not included in these comparisons because *T. acaciaelongifoliae* established there only in 1986 and because of the low weed status of A. *longifolia* in this province (Macdonald & Jarman, 1985).

Comparisons show that the differences in establishment and infestation levels between the South African regions distinguished above were highly significant. *Trichilogaster acaciaelongifoliae* established best in the coastal south-western Cape Province (Table 15, above). Although establishment in the southern Cape was not as good as in the coastal south-western Cape, establishment in both of these areas was much more successful than in the inland valleys and west coast of the south-western Cape, and Natal. There was no difference in the degree of establishment in the latter two regions.

Comparison of the final scores for levels of infestation in these regions (excluding Natal) shows that infestation levels in the southern Cape had improved since establishment and did not differ from the coastal south-western Cape. However, infestation levels in both of these regions were still much higher than in the inland valleys and west coast of the south-western Cape (Table 16). The scores on which these comparisons are based are mapped in Figs. 26 & 27.

TABLE 16 Comparison of the final scores for the levels of infestation of *T. acaciaelongifoliae* on *A. longifolia* at the release sites in (1) the inland valleys of the south-western Cape Province, (2) the coastal south-western Cape Province and (3) the southern Cape Province. Avg. = average, min. = minimum, diff. = difference.

Region	n	Rank avg.	Comparison	Avg. diff.	Min. diff. (P<0.0001)
1	20	15.9	1 vs. 2	46.7	> 11.3
			1 vs. 3	41.4	> 11.6
2	42	62.5	2 vs. 3	5.2	< 9.3
3	37	57.3			

A comparison of the coastal and inland valleys of the south-western Cape over a three year period shows that establishment and levels of infestation in the inland valleys were consistently poorer than in the coastal regions after releases in 1983 (Table 17). Moreover, the scores for the former region declined steadily over the study period in contrast to the increasing scores for the latter region.

TABLE 17 Comparison of the degree of establishment and levels of infestation of *T. acaciaelongifoliae* on *A. longifolia* in (I) the inland valleys (n = 20 sites) and (2) the coastal regions of the mediterranean south-western Cape Province (n = 42 sites) from 1984 until 1986. Avg. = average.

Year	Rank avg.		Level of significance for difference
	Inland	Coastal	
1984	18.6	37.6	<0.0001
1985	17.3	37.7	<0.0001
1986	12.2	42.2	<0.0001

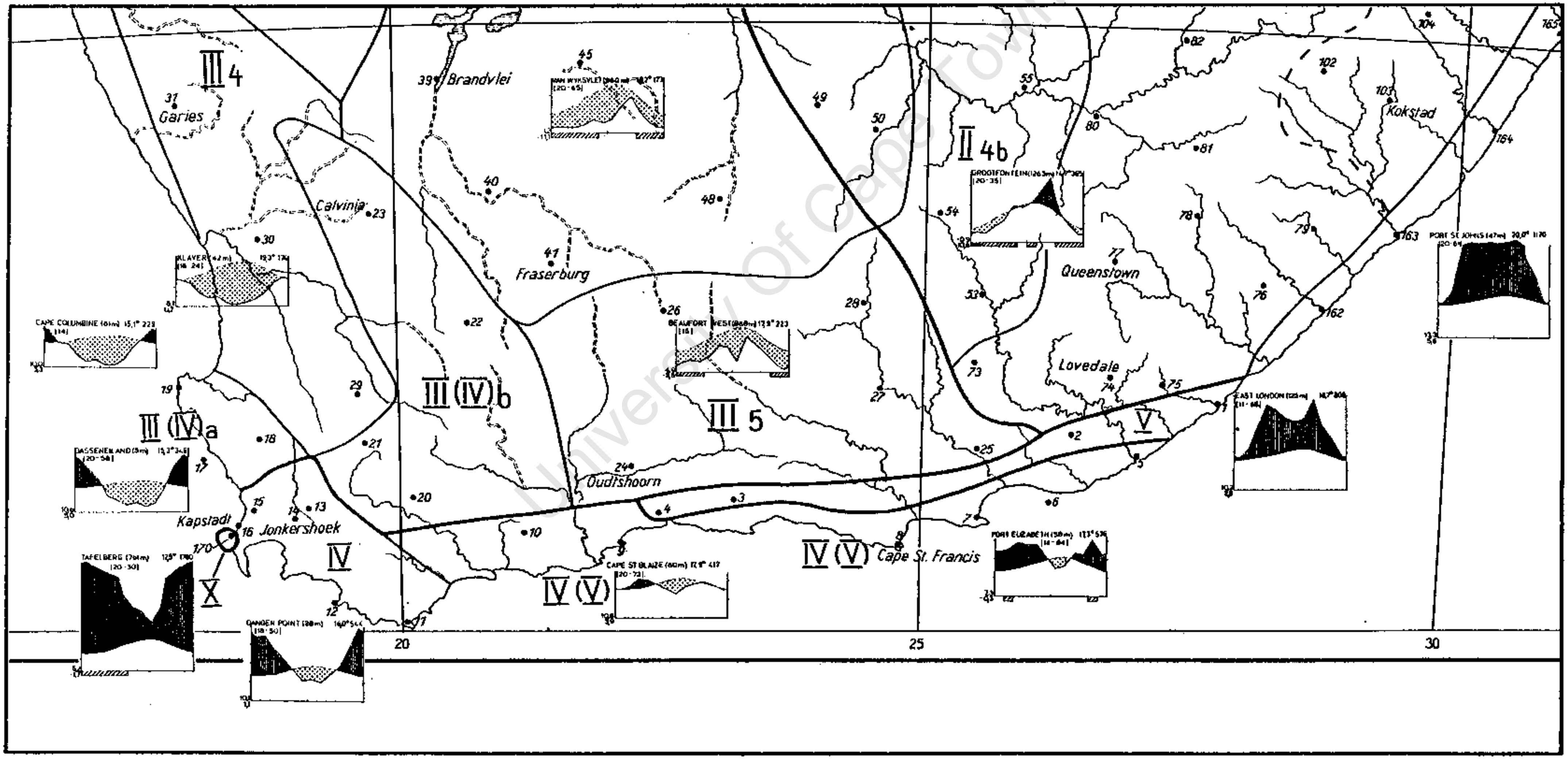
The climatic classification of the south-western and southern Cape Province according to Walter & Leith (1960) is given in Figure 28. According to this classification, the regions in which *T. acaciaelongifoliae* is successful fall in the climatic types IV, IV(V), and V, whereas the regions in which the performance of the wasp is poor fall within the major climate type HI (III(IV)a, III(IV)b and III(4)) of Walter & Leith (1960) (Figs. 29 & 30). The Klimadiagrams of Walter & Leith (1960) show that the areas in which *T. acaciaelongifoliae is effective* - types IV and V - have no arid period or a relatively short arid period in midsummer (Fig. 31). In contrast, the areas in which the wasp is functioning poorly - type III - have longer summer aridity and a greater difference between winter and summer temperatures with summer temperatures being relatively higher (Fig. 31).

All of the sites where *T. acaciaelongifoliae* was collected in south-eastern Australia (Table 14, above) fall within the major climate types IV and V of Walter & Leith (1960), with Melbourne approaching a midsummer aridity and Launceston having a very short arid period in midsummer (Fig. 32). Areas with a proper mediterranean climate similar to that of the coastal south-western Cape Province of South Africa occur in the coastal regions west of Melbourne to Adelaide (Fig. 32). Australian areas corresponding to the hot inland valleys of the south-Western Cape Province occur inland where New South Wales, Victoria and South Australia border on each other:

The climatic classification of Köppen (1900) for South Africa is given in Figure 33A. According to this classification, the regions in which *T. acaciaelongifoliae is effective* in South Africa have climate types Csb (coastal south-western Cape) and Cfb (southern Cape), whereas the regions in which the wasp is ineffective fall mainly in climate type Csa (Figs. 34 & 35). Climate type Csa is distinguished from climate type Csb (and Cfb) because the mean temperature for the warmest month is over 22 °C for Csa whereas it is below 22 °C for Csb and Cfb. All of the sites from which *T. acaciaelongifoliae* was collected in Australia fall within climate type Cfb (Fig. 33B) *i.e.* areas where the mean maximum temperature is below 22 °C.

A comparison of the average daily maximum and minimum temperatures in the South African regions distinguished by the performance of *T. acaciaelongifoliae,* shows, as would be expected, that the inland valleys and west coast of the south-western Cape are substantially warmer during the summer months and colder in winter than both the coastal south-western and southern Cape Province (Fig. 36). The average daily maximum and minimum temperatures for the warmest and coldest months, respectively, in the areas where *T. acaciaelongifoliae* was collected in Australia are given in Table 18.

Fig. 28. The climate classification of the south-western and southern Cape Province of South Africa after Walter & Leith (1960).



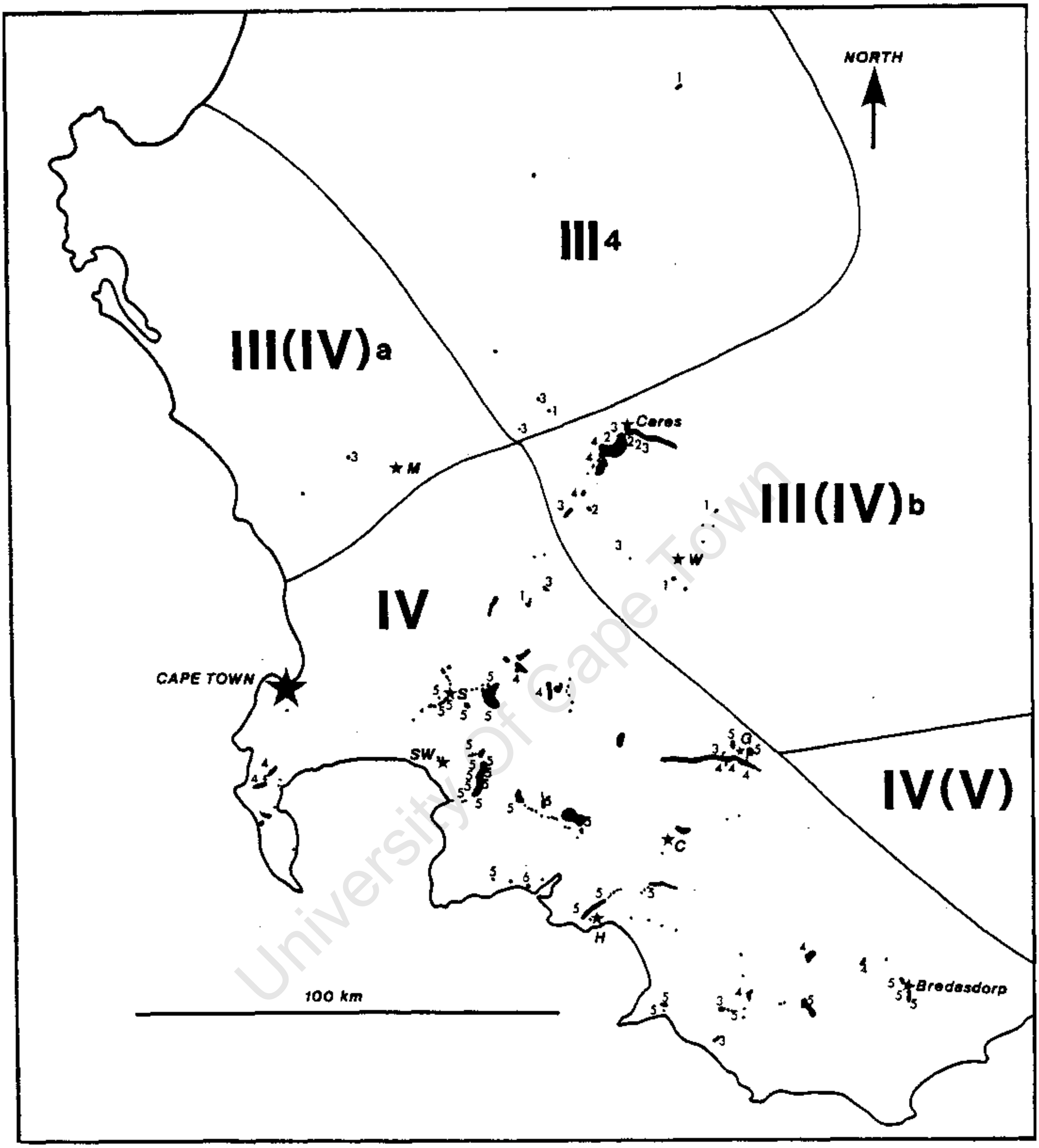


Fig. 29. The climate classification of Walter & Leith (1960) superimposed on the mapped levels of infestation of *T. acaciaelongifoliae* at release sites in the south-western Cape Province. For the key to towns represented by stars see Fig. 26.

Fig. 30. The climate classification of Walter & Leith (1960) superimposed on the mapped levels of infestation of *T. acaciaelongifoliae* at release sites in the southern Cape Province. For the key to towns represented by stars see Fig. 27.

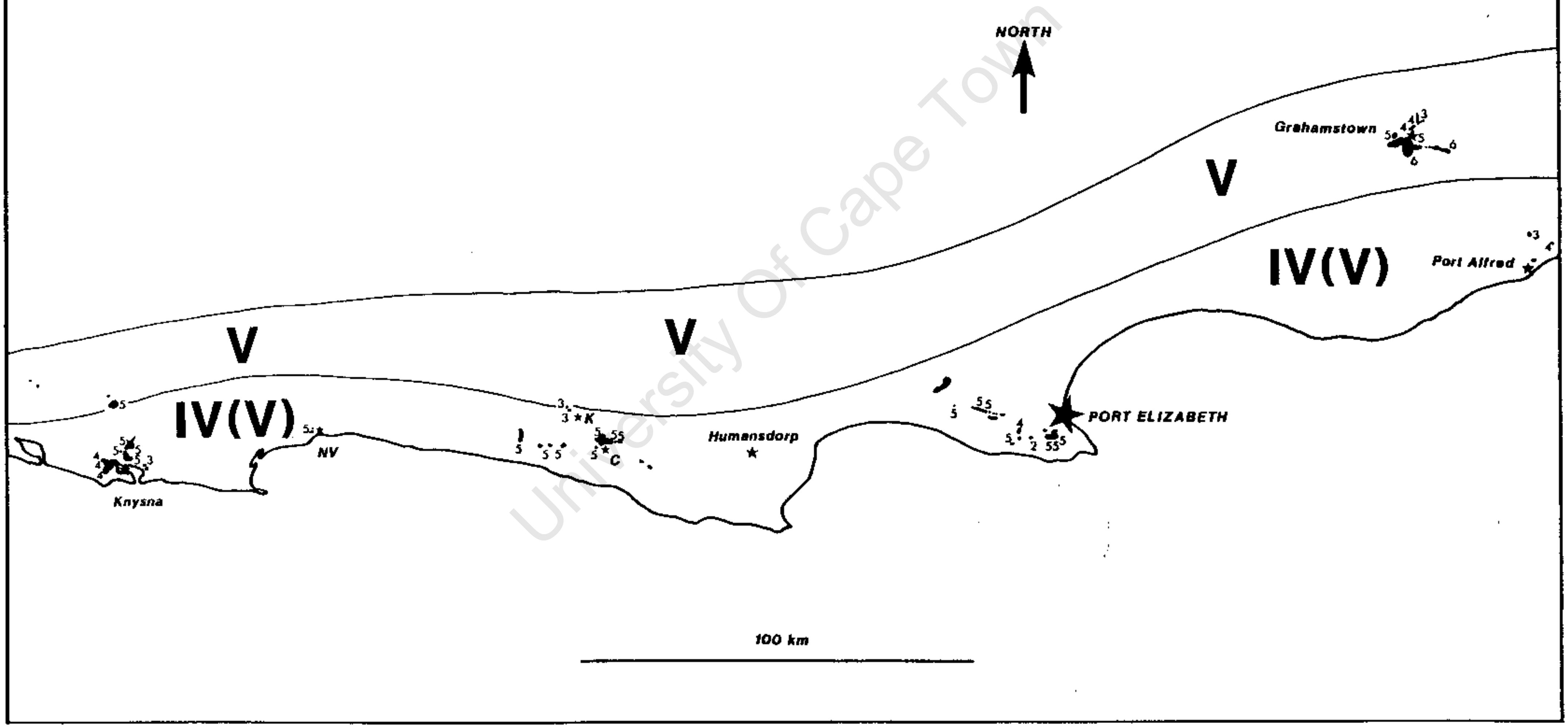
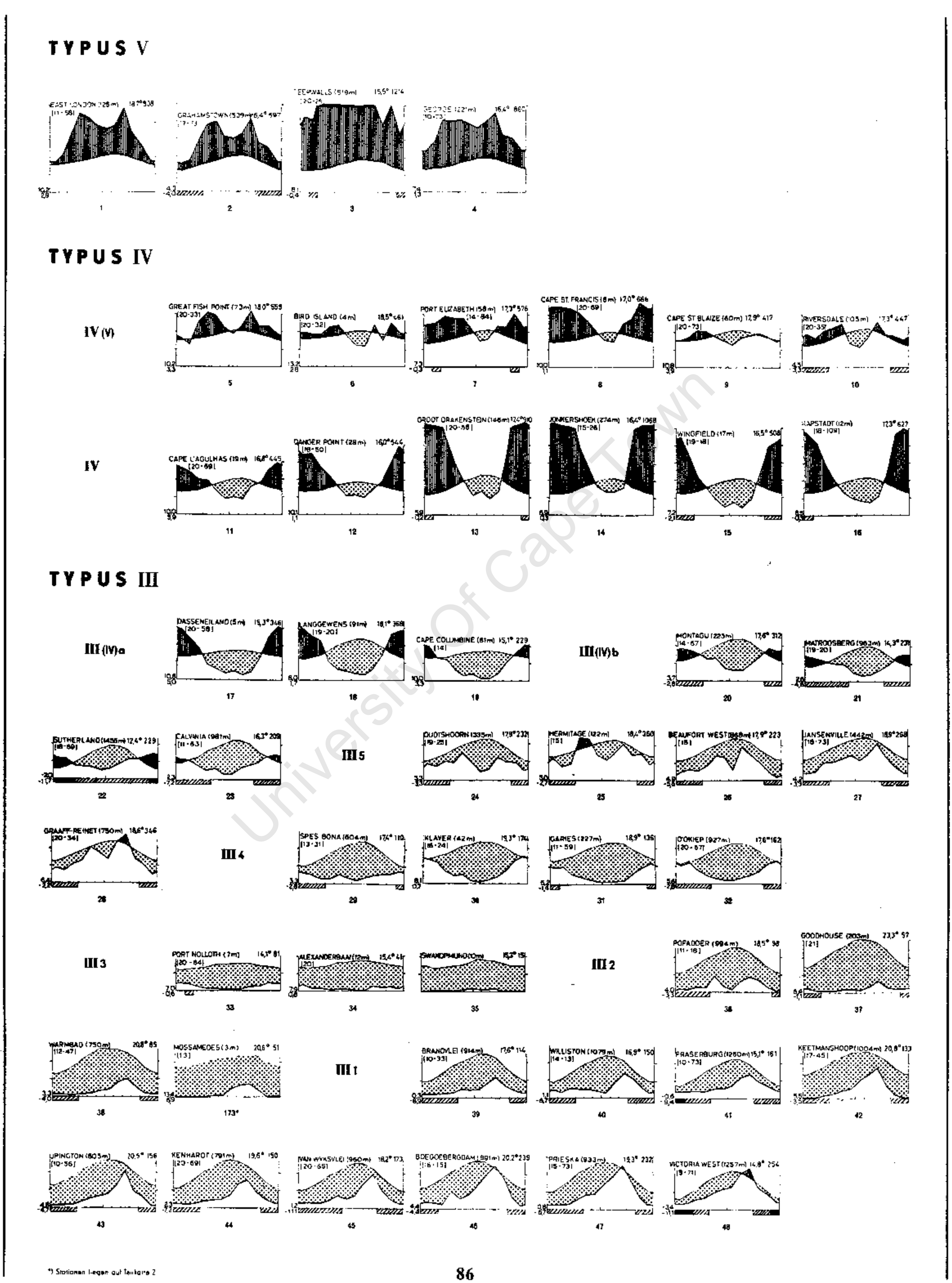
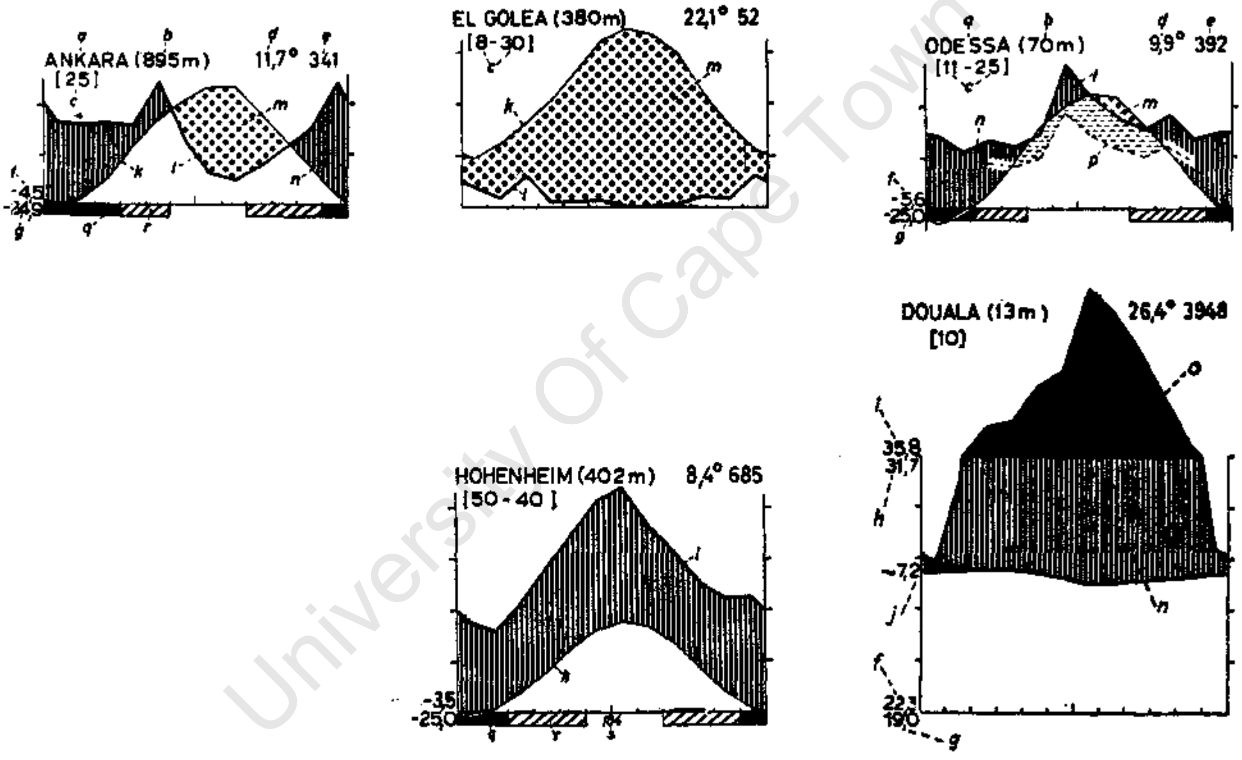


Fig. 31. Klimadiagrams copied from Walter & Leith (1960) for the climate types represented in Figs. 29 & 30. The key to this figure is given overleaf.



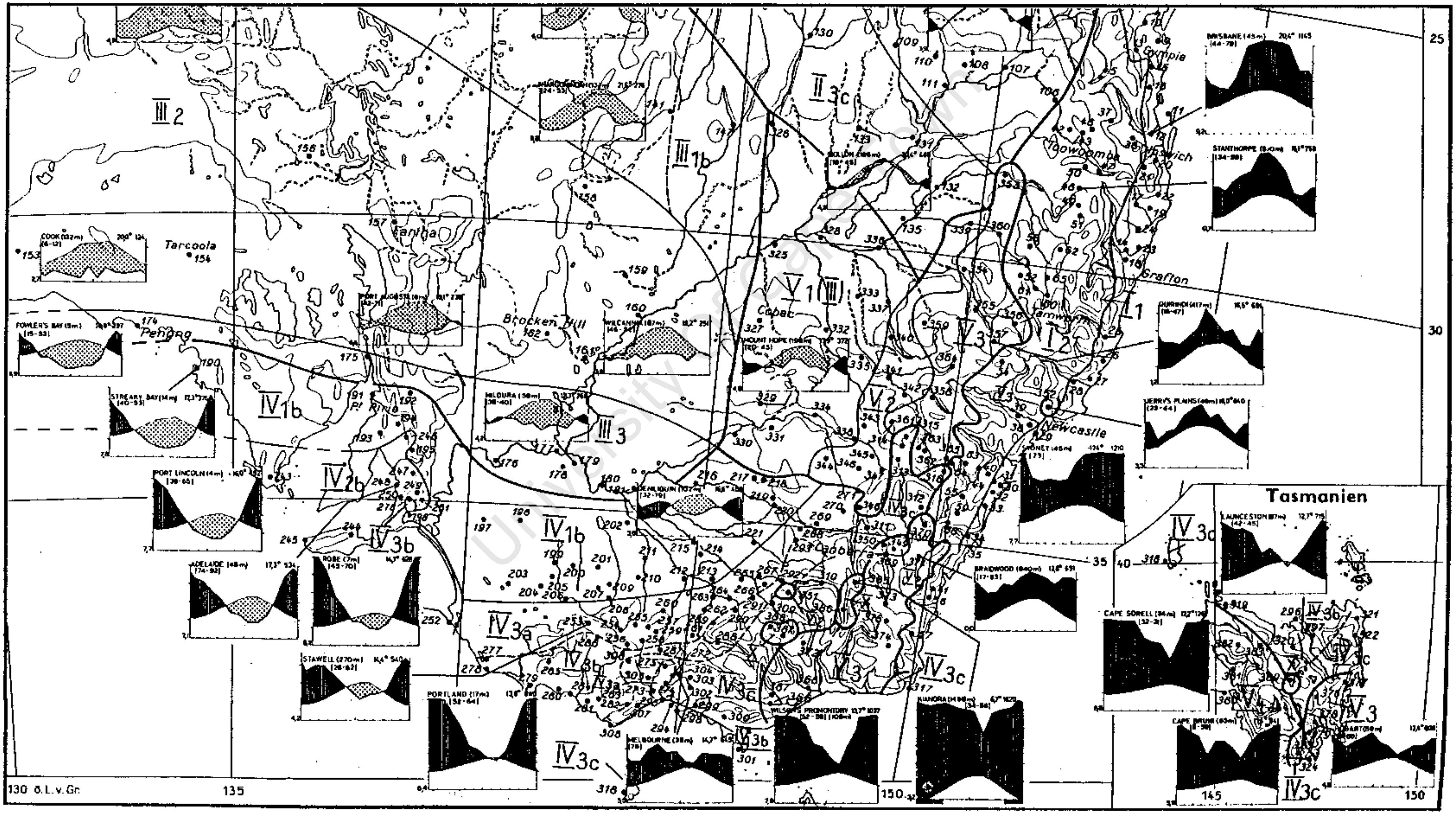
Key to Fig. 31, copied from Walter & Leith (1960).



Each of the letters of the alphabet used below stands for a certain meaning:

a — station
b — altitude
c — number of years of observation (the first stands for temperature, the second for precipitation)
d — mean annual temperature in degrees centigrade
e — mean annual sum-total of precipitation in mm
f — mean daily minimum of the coldest month
g — absolute minimum
h — mean daily maximum of the hottest month
i — absolute maximum
j — mean range of temperature

Fig. 32. The climate classification of south-eastern Australia and Tasmania after Walter & Leith (1960).



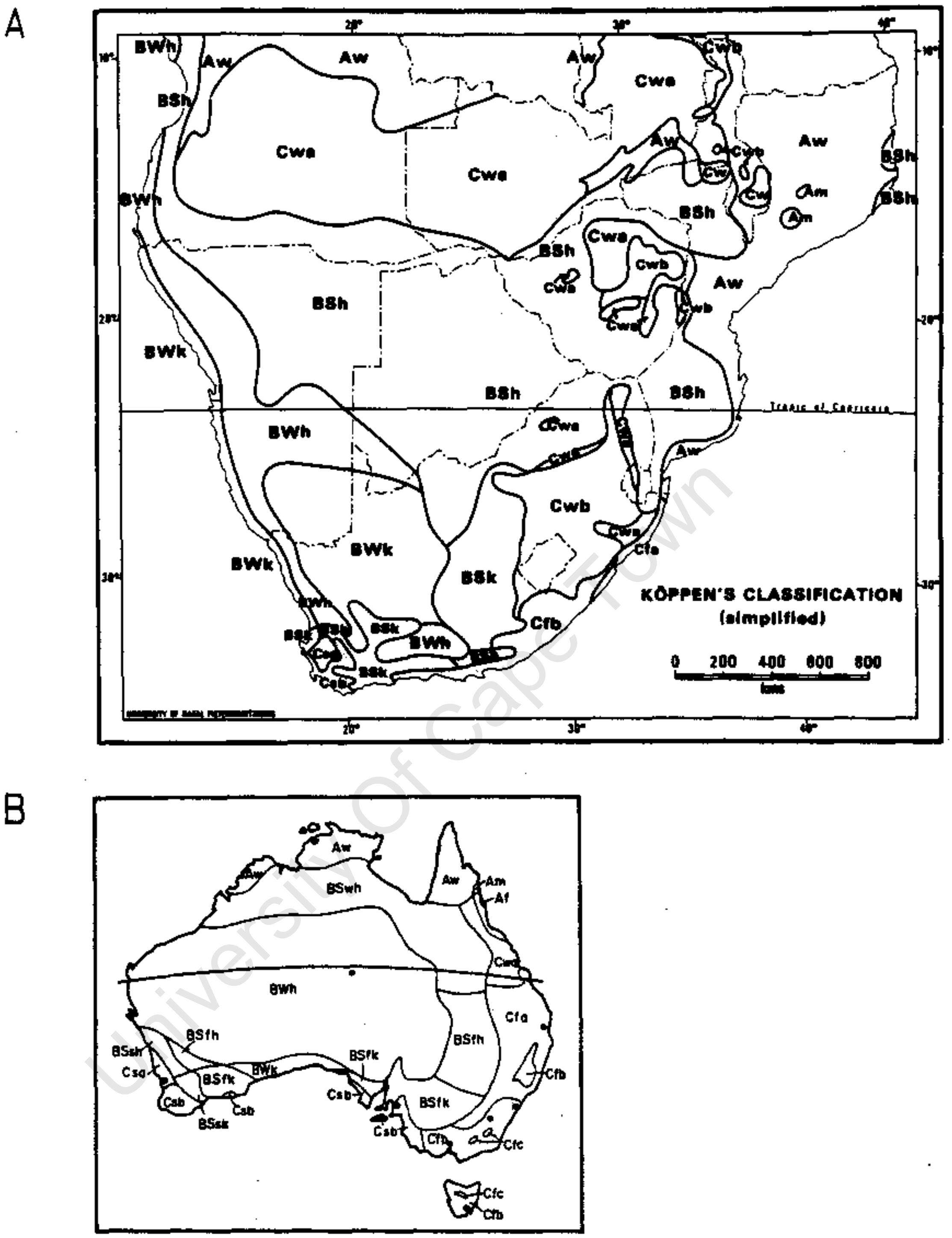


Fig. 33. Köppen's (1900) classifications of South Africa (A) and Australia (B) copied from Schulze & McGee (1978) and Linacre & Hobbs (1977), respectively. Key for the relevant regions (shaded in blue) : C = T(min) between -3 & 18 C, f = rain all months, s = dry summer, a = T(max) over 22 C, b = T(max) less than 22 C and not less than 4 months over 10 C, h = T(mean) over 18 C, dry.

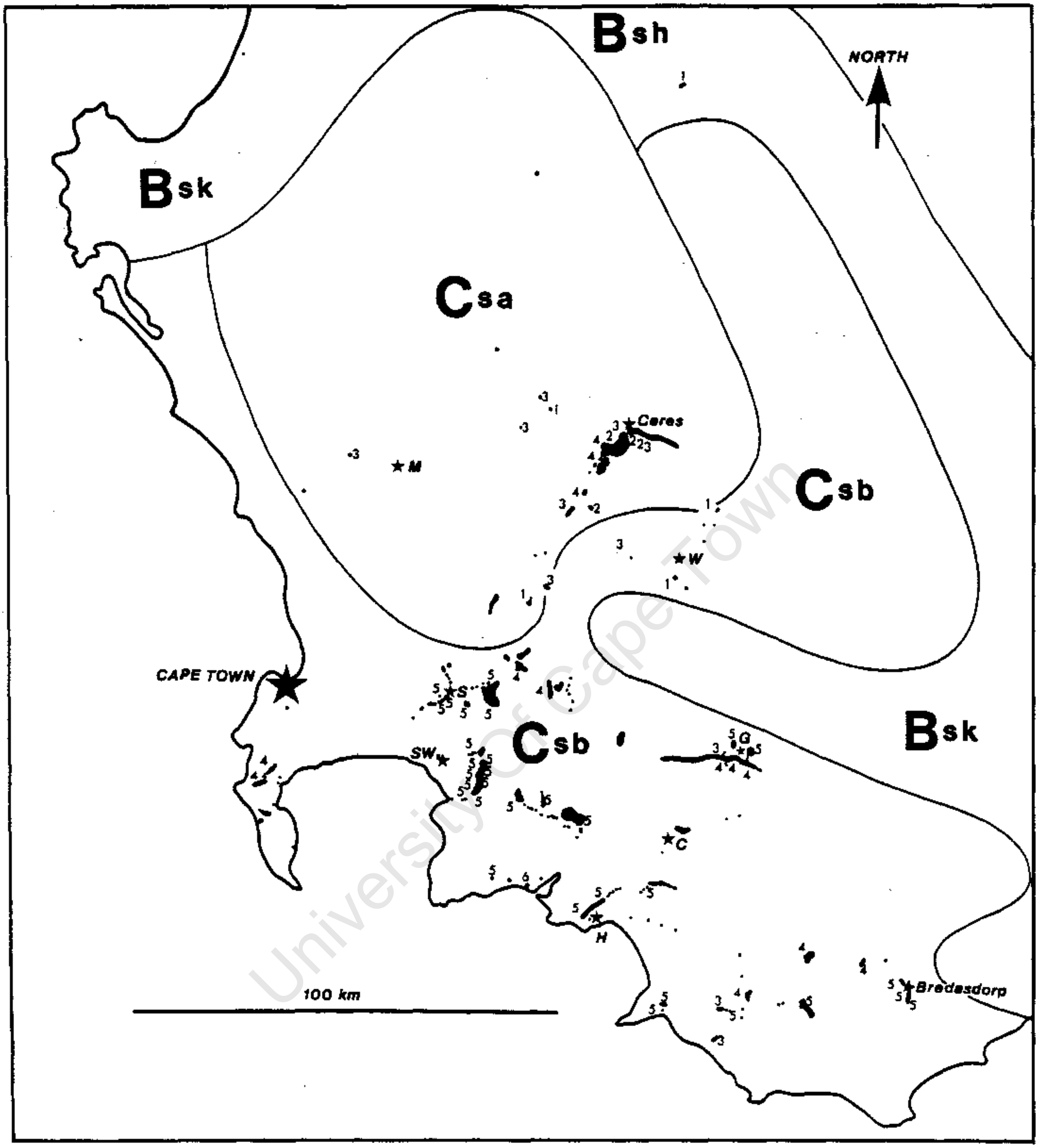
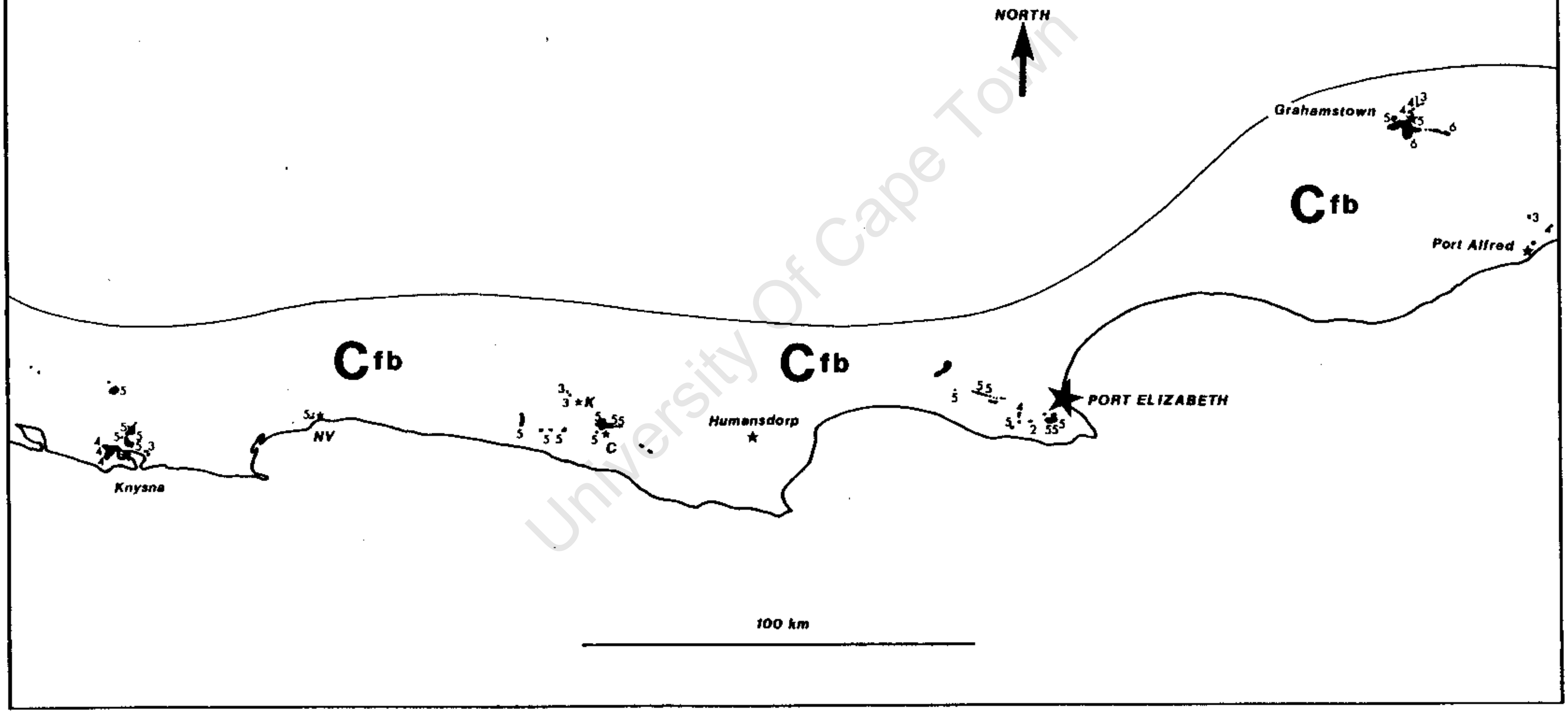


Fig. 34. The climate classification of Köppen (1900) superimposed on the mapped levels of infestation of *T. acaciaelongifoliae* at release sites in the south-western Cape Province. For the key to towns represented by stars see Fig. 26.

Fig. 35. The climate classification of Köppen (1900) superimposed on the mapped levels of infestation of *T. acaciaelongifoliae* at the release sites in the southern Cape Province. For the key to towns represented by stars see Fig. 27.



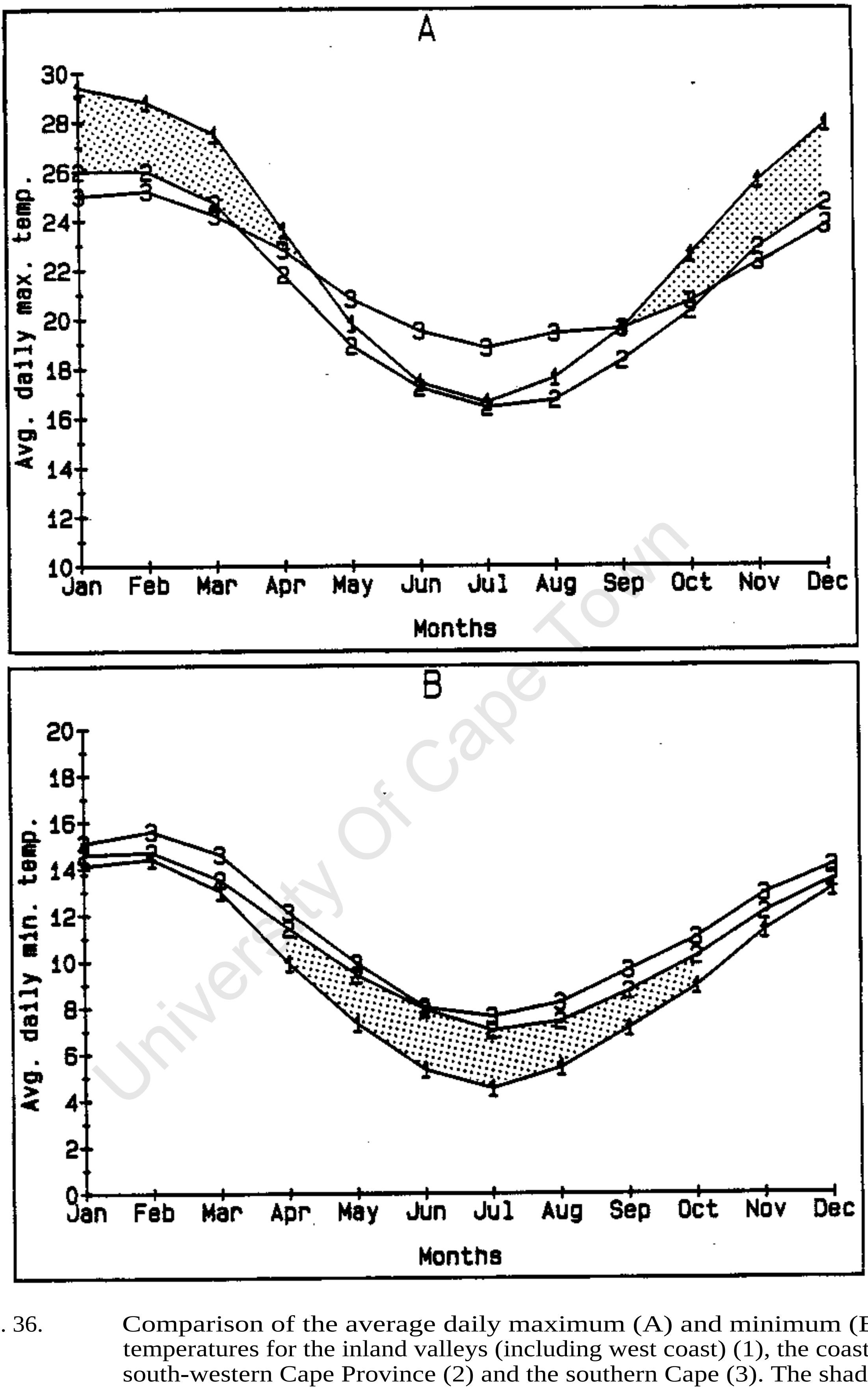
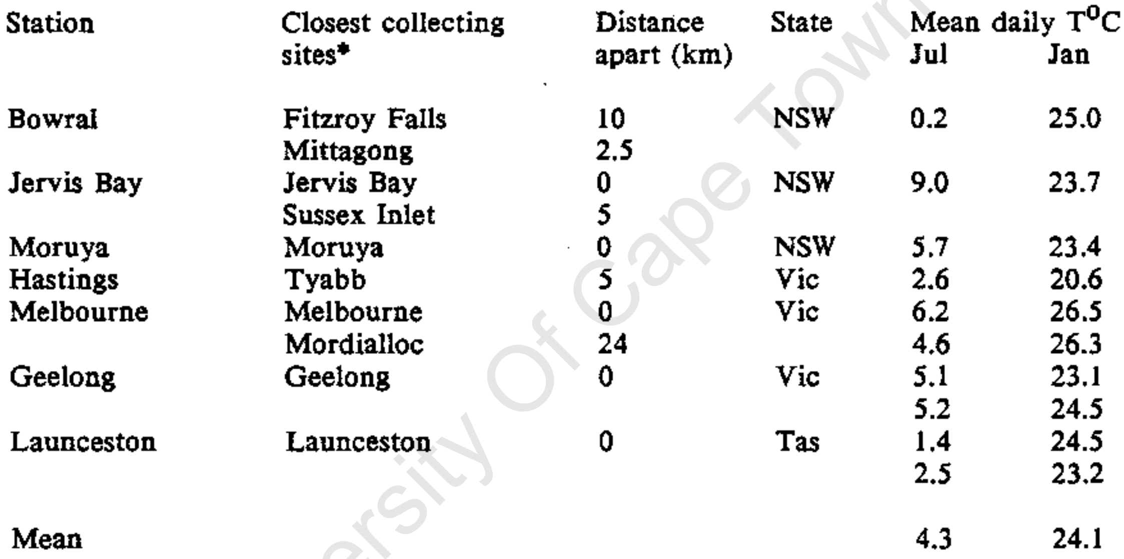


Fig. 36. Comparison of the average daily maximum (A) and minimum (B) temperatures for the inland valleys (including west coast) (1), the coastal south-western Cape Province (2) and the southern Cape (3). The shaded areas illustrate the months during which region 1 differs significantly ($P < 0.05$) from regions 2 and 3.

These show that the wasp should not be limited by the low winter temperatures experienced in the inland valleys in the south-western Cape (Fig. 36B), but that it may indeed be limited by the high summer temperatures experienced there (Fig. 36A). In confirmation, over 95% of the wasps imported in 1982 and subsequently used for nationwide releases in South Africa came from the sites within the 20 to 25 °C homocline for January average maximum temperature (Gentilli, 1971).

TABLE 18 The average daily minimum and maximum temperatures for July and January, respectively, at weather stations closest to the sites at which *T. acaciaelongifoliae* was collected in south-eastern Australia and Tasmania. NSW = New South Wales, Vic = Victoria, Tas = Tasmania, * = the collecting sites represented are given in Table 14.



Station	Closest collecting sites*	Distance apart (km)	State	Mean daily T°C Jul	Jan
Bowral	Fitzroy Falls	10	NSW	0.2	25.0
	Mittagong	2.5			
Jervis Bay	Jervis Bay	0	NSW	9.0	23.7
	Sussex Inlet	5			
Moruya	Moruya	0	NSW	5.7	23.4
Hastings	Tyabb	5	Vic	2.6	20.6
Melbourne	Melbourne	0	Vic	6.2	26.5
	Mordialloc	24		4.6	26.3
Geelong	Geelong	0	Vic	5.1	23.1
				5.2	24.5
Launceston	Launceston	0	Tas	1.4	24.5
				2.5	23.2
Mean				4.3	24.1

DISCUSSION

Trichilogaster acaciaelongifoliae has been established throughout the range of *A. longifolia* in South Africa. Human interference has not adversely affected the survival of release sites. The excellent dispersal abilities of the wasp (Chapter 1; Dennill, 1987 in press; Appendix 2) coupled with the fact that most of the release sites are within 5 to 10 kilometers from each other will further minimise the effects of human disturbance.

The establishment of *T. acaciaelongifoliae* in the southern Cape was significantly lower than in the coastal south-western Cape. This is noteworthy because the southern Cape corresponds climatically most closely to the regions where the wasp was collected in Australia. The relatively poor establishment in this region (southern Cape) is

explained by the fact that the wasps were released there in 1984, the last year of one of the worst droughts that the region has had in recent times. However, the climatic suitablility of this area for *T. acaciaelongifoliae* was demonstrated by the fact that despite this relatively poor establishment, the subsequent levels of infestation (post drought) increased markedly and did not differ from the coastal south-western Cape Province within one wasp generation. Moreover, the climatic suitabiliy of this area (and perhaps the drought) account for the fact that the highest branch and tree mortalities occurred in this region in the year immediately succeeding both the establishment of *T. acaciaelongifoliae* and the drought.

Although *T. acaciaelongifoliae* has established throughout the range of *A. longifolia* in South Africa, there are climatically distinct regions in which the wasp appears to be less effective. The weed thus has a partial refugium which appears to be the result of releasing insects collected from Australian regions which have relatively low summer temperatures, and which consequently have a very short or no arid period. Circumstantial evidence points to the fact that high summer temperatures are limiting the success of *T. acaciaelongifoliae in* the South African areas concerned. Firstly, 18 of the 25 sites (72%) in this region are riverine, meaning that the *A. longifolia* trees suffer no water shortage. Secondly, all of the sites in this region that had a high score (4) for infestation level were shaded by taller trees of other species. Only one site with a high score was not shaded by trees of another species, but the high score for this site was the result of very heavy galling in the lower, shaded parts of the trees.

High summer temperatures probably result in mortality of *T. acaciaelongifoliae* eggs and early instar larvae. Plant tissue follows ambient temperature closely, and this has been shown to be so for gall tissue (Baust *et al.,* 1979; Uhler, 1951). Moreover, the egg stage of gall forming insects appears to be especially vulnerable (Clancy *et al.,* 1986; Price & Clancy, 1986; Price & Craig, 1984), and this is also true for a wider range of insects (White, 1969, 1974, 1976).

This study thus provides strong evidence that climatic pre-adaptation profoundly influenced the success of *T. acaciaelongifoliae* in different regions in South Africa. The climatic tolerances of the insect are, however, not that narrow ; although all the wasps released originated from areas most similar to the southern Cape, they established well and achieved high infestation levels in the distinctly mediterranean south-western Cape Province. The climate of the hotter areas of the south-western Cape is, however, clearly beyond the limits of tolerance for the insects used. *Acacia longifolia* also occurs along the coastal regions of South Australia up to Adelaide (Costermans, 1981). This region experiences a climate identical to that of the mediterranean south-western Cape,

and is closer to the inland regions of Australia which have a climate like that of the hot inland valleys of the south-western Cape. Moreover, Adelaide and surrounding regions fall within the 25 to 30 °C homocline for average daily maximum temperature for January (Gentilli, 1971). Although *A. longifolia* does not occur inland in Australia, insects originating from coastal South Australia with its higher summer temperatures and distinct summer aridity may be better adapted to cope with the conditions in the corresponding areas in South Africa.

Wilson (1949, 1964) and Wapshere (1970a, 1970b, 1974) have stressed the importance of selecting eco-climatically adapted agents. These authors have been mis-construed as maintaining that eco-climatic matching alone is the basis for selecting biocontrol agents by Huffaker (1957) and Harris (1973). There is, however, evidence supporting eco-climatic matching (Caresche & Wapshere, 1975; Delfosse & Cullen, 1980; Harley, 1974; Pettey, 1948; Wilson, 1960; Zimmermann & Moran, 1982; Zimmermann *et al.*, 1986). Eco-climatic matching has received much attention in recent times (Wapshere, 1970a, 1970b, 1973, 1974). Since this principle was re-emphasised and placed in context with other considerations regarding the selection of biocontrol agents by Sands and Harley (1980), it has been re-instated in Goeden's (1983) and Wapshere's (1985) revisions of Harris' system for rating the potential of biocontrol agents for weeds. This is not at all surprising since, as Sands and Harley (1980) point out, this is only a practical application of the generally accepted concept of climatically adapted sub-species or races (Mayr, 1971). The present study supports the view that eco-climatic matching is important, at least in the case of some agents.

TABLE 19 Descriptions and co-ordinates of the 139 sites throughout the South African range of *A. longifolia* to which *T. acaciaelongifoliae* was distributed in 1983 and 1984.

No.	Site description	Co-ordinates
SOUTH-WESTERN CAPE PROVINCE		
1	Grootrivier bridge	32°39'S;19°25'E
2	Ceres refuse dump	33°23'S;19°18'E
3	Ceres at bridge over Titus River	33°23'S;19°19'E
4	Bergtoppe	33°23'S;19°20'E
5	Dwarsberg on Titus River	33°24'S;19°22'E
6	Vergenoeg on Titus River	33°24'S;19°24'E
7	Mitchell's Pass near summit	33°23'S;19°17'E
8	Witels picnic site in Mitchell's Pass	33°25'S;19°17'E
9	Junction of Tulbagh, Wolsely and Worcester roads	33°25'S;19°16'E
10	Wolsely/Worcester road	33°26'S;19°13'E
11	Romansrivier near prison	33°28'S;19°12'E
12	Waterval on Tulbaghweg	33°20'S;19°07'E
13	In poort between Gouda & Tulbagh	33°18'S;19°04'E
14	Voelvlei yacht club	33°22'S;19°02'E
15	Klein Bergrivier bridge	33°13'S;18°59'E
16	Mamreweg	33°26'S;18°38'E
17	Mamre	33°31'S;18°29'E
18	Bainskloof on Worcester side	33°34'S;19°09'E
19	Bridge over Breerivier at bottom of Bainskloof	33°31'S;19°11'E
20	Bridge over Breerivier to Slanghoek	33°32'S;19°12'E
21	Bridge over Jan du Toit's River	33°36'S;19°19'E
22	Breerivier at bridge to Rawsonville	33°41'S;19°25'E
23	Poort between Hex River valley and Worcester	
24	Top of Du Toit's Kloof Pass near flower shop	33°43'S;19°05'E
25	Du Toit's Kloof Pass bottom Paarl side	33°44'S;19°05'E
26	Banhoek Valley	33°57'S;18°58'E
27	Banhoek Valley near Kylemore	33°56'S;18°58'E
28	Bridge over Berg River to Franschhoek	33°53'S;19°02'E
29	La Motte State Forest	33°55'S;19°03'E
30	Stellenbosch Mountain	33°57'S;18°54'E
31	The Boord (Stellenbosch)	33°57'S;18°51'E
32	Vredenburg (outside Stellenbosch)	33°57'S;18°50'E
33	Papegaaiberg	33°56'S;18°50'E
34	Kirstenbosch	33°59'S;18°26'E
35	OranjeNek	34°01'S;18°23'E
36	Vergelegen	34°04'S;18°56'E
37	Knorhoek (a)	34°06'S;18°56'E
38	Knorhoek (b)	34°06'S;18°57'E
39	Knorhoek (c)	34°06'S;18°57'E
40	Knorhoek (d)	34°07'S;18°57'E

41	Knorhoek (e)	34°07'S;18°57'E
42	Knorhoek (f)	34°08'S;18°57'E
43	Sir Lowry's Pass at bottom	34°08'S;18°56'E
44	Sir Lowry's Pass at summit	34°09'S;18°56'E
45	National highway crossing of Palmiet River near Grabouw	34°10'S;19°01'E
46	Lebanon Forest	34°11'S;19°08'E
47	Houhoek	34°12'S;19°09'E
48	Palmiet River at coast	
49	Mouth of Bot River at Kleinmond	34°20'S;19°02'E
50	Otto Du Plessis bridge in valley behind Hermanus	34°24'S;19°13'E
51	Shaw's Pass bottom	34°22'S;19°16'E
52	Shaw's Pass top	34°21'S;19°23'E
53	Farm near Baardskeerdersbos	34°34'S;19°33'E
54	Baardskeerdersbos village	34°35'S;19°33'E
55	Turnoff from coastal road to Franschekraal	34°36'S;19°23'E
56	Franschekraal at foot of mountain	34°35'S;19°23'E
57	In pass from Pearly Beach to Elim	34°38'S;19°35'E
58	Nuwedam near Baardskeerdersbos	34°35'S;19°36'E
59	Die Heer se Bos at Elim	34°35'S;19°45'E
60	Die Skeiding between Napier and Elim	34°28'S;19°46'E
61	Napier	34°29'S;19°55'E
62	Brickfields between Napier and Bredasdorp	34°32'S;20°02'E
63	Bredasdorp on Napier side	34°31'S;20°02'E
64	Bredasdorp on Agulhas side (a)	34°33'S;20°02'E
65	Bredasdorp on Agulhas side (b)	34°33'S;20°02'E
66	On Riviersonderend	34°04'S;19°28'E
67	Meulrivier crossing on Riviersonderend road	34°03'S;19°29'E
68	Voorstekraal	34°03'S;19°32'E
69	Genadendal in valley behind town	34°02'S;19°34'E
70	Greyton on river at end of Nerina Street	34°02'S;19°37'E
71	Greyton at Caledon turnoff	34°03'S;19°37'E

SOUTHERN CAPE PROVINCE

72	National highway at entry to Knysna Lagoon	34°03'S;22°59'E
73	Belvedere	34°02'S;22°60'E
74	On mountain drive to Brenton on Sea	34°02'S;22°59'E
75	Karatara State Forest Nols se Kop	33°53'S;22°59'E
76	Knysna on road to Mount Joy	34°02'S;23°03'E
77	Knysna Mount Joy	34°02'S;23°03'E
78	Knysna behind Royal Hotel	34°02'S;23°03'E
79	Knysna behind Hospital	34°02'S;23°04'E
80	Knysna turnoff to Port Elizabeth	34°02'S;23°04'E
81	Knysna industrial area	34°02'S;23°04'E
82	Nature's Valley in village	33°59'S;23°33'E

83	Witels State Forest	33°59'S;24°08'E
84	National highway crossing of river at Witels State Forest	33°59'S;24°09'E
85	Oubos Rand	34°00'S;24°15'E
86	Near intersection of Witels/Clarkson road and national highway	34°01'S;24°18'E
87	Kareedouw at Oubosrand turnoff	33°57'S;24°16'E
88	Kareedouw opposite factory	33°57'S;24°16'E
89	Stream crossing on Clarkson road	34°01'S;24°20'E
90	Clarkson (a) near church	34°01'S;24°21'E
91	Clarkson (b) near church	34°01'S;24°21'E
92	Clarkson at stream in mountain behind village	34°01'S;24°21'E
93	Palmiet Vlei	34°02'S;24°26'E
94	30 km west of Humansdorp on N2	33°55'S;25°21'E
95	Port Elizabeth N2 at turnoff to St. Alban's	33°56'S;25°20'E
96	Port Elizabeth N2 Fairview	33°56'S;25°22'E
97	Port Elizabeth N2 Greenbushes flyover	33°57'S;25°25'E
98	Walmer Golf Course	34°00'S;25°33'E
99	Walmer near shops	34°00'S;25°33'E
100	Next to railway line at Bog Farm	33°59'S;25°33'E
101	Walmer fire station	33°58'S;25°34'E
102	Sardinia Bay road near old Seaview Road turnoff	34°01'S;25°30'E
103	Theesecombe	34°01'S;25°28'E
104	Bushy Park	34°01'S;25°25'E
105	Port Alfred at Kleinemond exit	33°35'S;26°55'E
106	Standerwick	33°32'S;26°55'E
107	Haye's Siding	33°31'S;26°53'E
108	Grahamstown on Port Alfred road (a)	33°20'S;26°38'E
109	Grahamstown on Port Alfred road (b)	33°20'S;26°36'E
110	Grahamstown on Port Alfred road (c)	33°20'S;26°35'E
111	Grahamstown, opposite Calderwood	33°20'S;26°34'E
112	Grahamstown, Woest Hill	33°20'S;26°33'E
113	Grahamstown, picnic site below Settler's Monument	33°19'S;26°31'E
114	Grahamstown camp site	33°19'S;26°32'E
115	Grahamstown west next to railway line	33°19'S;36°30'E
116	KingWilliam's Town road (a) Collingham	33°16'S;26°38'E
117	KingWilliam's Town road (b) Bathurst State Forest	33°16'S;26°41'E
118	KingWilliam's Town road (c)	33°16'S;26°41'E
119	KingWilliam's Town road (d)	33°16'S;26°42'E
120	KingWilliam's Town road (e) opposite radio tower	33°16'S;26°43'E

NATAL

121	Paradise Valley next to N3	29°45'S;30°55'E
122	Near entrance to Paradise Valley Nature Reserve	29°45'S;30°55'E
123	Hillcrest turnoff from N3	29°45'S;30°45'E
124	Pietermaritzburg Town Bush road near bus stop on way to Harris water plant	29°35'S;30°20'E
125	Harris water purification plant	29°35'S;30°20'E
126	Hilton turnoff from old Howick road	29°35'S;30°15'E
127	Midmar Dam entrance	29°30'S;30°10'E
128	Old Howick road near N3	29°30'S;30°15'E
129	Sweetwaters railway crossing	29°40'S;30°15'E
130	Bluegum plantation at Sweetwaters	29°40'S;30°15'E
131	Crompton Road turnoff from Sweetwaters road	29°35'S;30°15'E
132	N3 Town Hill	29°35'S;30°15'E
133	High Flats gum plantation near Ixopo (a)	30°15'S;30°10'E
134	High Flats gum plantation near Ixopo (b)	30°15'S;30°10'E
135	Next to dam on Ixopo/Umzinto road	30°15'S;30°35'E
136	Umzinto turnoff from Ixopo/Scottburg road	30°15'S;30°35'E

CHAPTER 6

Practical and theoretical implications

ABSTRACT

The present study is placed in context with the literature on gall insects, and that for the use of seed reducing agents in biological weed control. The implications of this project for the future control of *A. longifolia* in South Africa are discussed. Critical assessment of the theory of biological weed control in terms of the present project highlights deficiencies in that theory, which are shown to result mainly from inadequate evaluation of agents subsequent to their release. The success of the biological control of *A. longifolia* by *T. acaciaelongifoliae is* shown to be the combined result of certain features of (a) the gall wasp, (b) the weed, and (c) the interaction between the two. In addition, practical features (regarding the collection, transportation, rearing and releasing of the agent) which contributed to the success of this project are discussed. Of the ecologically important features, some confirm attributes which are either universally or tentatively regarded as essential in successful biocontrol agents. However, some of these features provide new principles for the future selection of biocontrol agents for weeds. It is in the provision of such new principles that the future of biological control of weeds lies, and this is shown, in the present case, to be founded on the detailed evaluation of the effects of the agent *T. acaciaelongifoliae* on its host plant *A. longifolia.*

Within the field of biological weed control, this thesis reports a successful biological control project that has relied on reduction of the weed's reproductive potential by an imported insect. The use of agents that inhibit reproduction has been regarded with some scepticism by several authors (see Goeden, 1983; Harris, 1973; Huffaker, 1957; Wilson, 1949). There are two reasons for this scepticism. Firstly, insects which reduce biomass or destroy existing stands of a weed are regarded as most suitable. Secondly, many weeds, including *A. longifolia,* are perennial and have a large and long-lived seed bank. Attempting to control these weeds by reducing seed production is regarded as futile. However, in the case of *A. longifolia,* recent research has shown that the longevity of the seed bank is not as formidable an obstacle as anticipated because it is markedly depleted (by about 90%) by fires which either kill seeds or stimulate germination (Pieterse, 1986). Moreover, in the *case* of *T. acaciaelongifoliae,* and other *effective* seed reducing agents, reduction of the density of the weed populations may be achieved in generations of the weed *subsequent* to those attacked. Such evidence has already been provided from a project in which a seed attacking weevil has reduced the density of a silky hakea, *H. sericea,* population by approximately 90% (Neser & Kluge, 1986).

In addition, the action of *T. acaciaelongifoliae* is to be augmented by a seed-feeding weevil *Melanterius ventralis* Lea (Donnelly, in prep.) which should further reduce the reproductive potential of *A. longifolia.* In the long term, the programme is viewed as an integrated one whereby the reduction in density of the weed will be achieved using seed reducing agents and fire. In the interim it must be emphasised that the aim of introducing *T. acaciaelongifoliae* and *M. ventralis* has primarily been to reduce the rate of spread of this invasive alien. The logical basis for this endeavour has already been discussed.

This study has shown that the advantage of an agent (like *T. acaciaelongifoliae)* which reduces seed production by gall formation is that reproductive potential (invasiveness), growth, and biomass are simultaneously reduced. In addition, the wasp holds potential for the longer term reduction in weed density by being compatible with the integrated programme described above.

The large volume of work that has been done on insect induced galls on plants has been reviewed by Felt (1940), Mani (1964) and most recently, and comprehensively, in Ananthakrishnan (1984). Shorter reviews are provided by Bloch (1953), Braun (1969), and Dixon (1983). Most of the research reviewed by these authors is of a descriptive, histological or biochemical nature. Ecological research on the interaction between gall forming insects and their hosts is a relatively recent field and appears to have had two motivating forces: biological weed control and the rapidly growing interest in plant/insect interactions (see Crawley, 1983 and Strong *et al.,* 1984).

In biological weed control, most research concerns the use of gall forming Tephritidae, and much of this has been reviewed by Freidberg (1984). Harris' (1980b) evaluation of the effectiveness of certain tephritids introduced from Europe to Canada to control knapweeds and Cullen *et al.* (1982) on the effects of the gall mite on skeleton weed are excellent examples of how biological weed control can provide ecological information regarding the interaction between gall formers and their hosts. Not all such work has been initiated in biocontrol circles, however, and the present study on *T. acaciaelongifoliae* and *A. longifolia* can be included with the following works which show that gall forming insects can have profound effects on the allocation of resources of their host plants: Craig *et al.* (1986), Harris (1980b), Hartnett & Abrahamson (1979), Price & Clancy (1986), Skuhravl *et al.* (1980), Stinner & Abrahamson (1979) and Weis & Kapelinski (1984).

Before examining the specific contributions of this thesis to the theory and practice of biological weed control, it is necessary to discuss the key issues being addressed in that theoretical literature. While doing this, I will also critically assess that theory in terms of the present project, and thereby provide general implications of this research for the theory of weed biocontrol.

GENERAL IMPLICATIONS FOR THE THEORY AND PRACTICE OF SELECTING EFFECTIVE BIOCONTROL AGENTS FOR WEEDS

The number of papers that have been written about the selection of biocontrol agents for weeds greatly exceeds the number of biocontrol agents whose effectiveness has been quantitatively evaluated subsequent to their introduction. Perusal of the reference lists accompanying the world catalogues of weed biocontrol by Julien (1982) and Maw (1984) confirms this. Because of this profusion of theoretical literature, I restrict this discussion to key papers, and direct the reader to Hokkanen (1985a) for a comprehensive and well written review of this surprisingly large body of literature.

On the concept of success in biocontrol

A successful biocontrol agent is classically regarded as one which will reduce the population density of the weed to an economically tolerable level (Huffaker, 1957). Reduction of weed density has, however, not always been that easily achieved (Harris, 1981). The effects of many successful agents have been more subtle, and subsequent definitions of successful biocontrol have had to be refined accordingly. Harris (1981) has pointed out that most agents stress but do not kill their hosts, and suggests that agents which are able to measurably increase stress load on the target weed should be regarded as successful. Julien *et al.* (1984) defined effective agents as those which contribute to the control of the weed. Wapshere (1985) regards an agent as successful if it is able to reduce the population or biomass of the weed below economically important levels. DeBach (1964) stated more srongly that the success of biocontrol agents be assessed by the economic savings resulting from their introduction. This definition is endorsed by Hokkanen (1985a). Hokkanen (1985a) has, however, emphasised both the importance and the difficulty of assessing success economically and warns against confusing economic success with ecological success (success of establishment).

In the present study, *T. acaciaelongifoliae* is regarded as a successful agent in a number of senses. Firstly, the wasp was ecologically successful because it established

readily throughout the range of the weed. Secondly, *T. acaciaelongifoliae* is successful because detailed studies have shown (a) that the wasp has strong potential to reduce reproductive and growth potential of *A. longifolia* (Chapters 2 & 4; Dennill, 1985 & 1988b in press; Appendices 1 & 4), (b) that actual reductions of seed production in A. *longifolia* populations are high (>73% and >83% at two sites) (Chapter 1; Dennill, 1987 in press; Appendix 2) and (c) that these levels of seed reduction are being achieved throughout the two South African regions in which *A. longifolia* is most invasive (Chapter 5). Thirdly, *T. acaciaelongifoliae* is successful *sensu* Harris (1981) and Wapshere (1985) in that it substantially increases the stress load on the plants (Chapters 2 & 4; Dennill, 1985 & 1988b in press; Appendices 1 & 4) which leads to a reduction in biomass, thus diminishing the competitive ability of this plant. Fourthly, the wasp is showing signs of qualifying for the classical definition of success (reducing weed density) since it has already caused mortality of *A. longifolia* trees at four sites.

To judge the effectiveness of *T. acaciaelongifoliae* by the attainment of a certain economic threshold is extremely difficult and to a large degree inappropriate. This is so because the losses attributable to *A. longifolia* are so difficult to express in pecuniary terms for two reasons. Firstly, the aesthetic value placed on the numerous conservation areas invaded and species threatened by the presence of this weed cannot be translated into financial terms. Secondly, hydrological disturbance is the only feature of this weed's invasiveness that could be expressed financially, and even so with great difficulty. At this stage the reduction of streamflow caused by alien plants can only be inferred from the effects of afforestation, and can be as high as 50% in fynbos (Versfeld & van Wilgen, 1986). The cost of clearing *A. longifolia* by an integrated programme involving mechanical and chemical means is conservatively estimated at R500 to R750 (=250 to 375 US $, respectively) per hectare (Ruddock, pers. comm.). Approximately 1157600 hectares of the fynbos biome alone (about 19% of the biome) is infested by *Acacia* and other thicket forming species (Macdonald *et al.* 1985). It is sufficient to say that *T. acaciaelongifoliae* is making an indeterminable but marked contribution to the saving of finances that would have been spent on mechanical control of the expanding *A. longifolia* populations if they were left unchecked.

While rigorous classical success, namely reduced weed density, is aimed at in the attempt to control *A. longifolia,* certain constraints have limited the programme to the use of 'indirect' control by reduction of seed production. The conflicting interests with the black wood and black wattle industries (Neser & Moran, 1985) and the difficulty of finding suitably host specific agents which inflict more direct damage (Donnelly, 1986) have aleady been discussed in this regard. The purpose of repeating this here is that the *aim* in introducing *T. acaciaelongifoliae* was to achieve reduction in seed production and thereby reduce the rate of spread of the weed *sensu* Harper (1977). This has been achieved in addition to the other effects described above. Thus the most relevant sense in which *T. acaciaelongifoliae* has been a successful or 'good' biocontrol agent is that it *has achieved the aim for which it was introduced.* In the context of biocontrol `successful', 'efficient', 'effective' and 'good' are synonomous, and Mackie's (1983) general definition of 'good' applies *i.e.* a 'good' biocontrol agent would be one which *satisfies requirements of the kind in question.*

In conclusion, *T. acaciaelongifoliae is* an agent which has been successful. However, the nature of this success cannot be captured in toto by any one of the accepted definitions of this term (success/effectiveness). It is suggested here that success in biocontrol be defined in terms of the achievement of the particular aims specified. Ironically, the more general nature of this way of defining success has the advantage of allowing one to define the success of particular agents more accurately ; those who are able to define success in financial terms are free to do so while others can apply whatever criteria they deem applicable. Because the aims of each biocontrol project are unique, universal definitions of success using particular criteria will always be of limited use.

On the selection of agents

Harris (1973) critically reviewed the major approaches to the selection of agents that were currently used at the time, and attempted to unify the principles used to provide a system whereby the successfulness of a potential agent could be predicted. According to this system the potential agent is scored on each key feature *e.g.* fecundity, damage inflicted to weed, phenology of attack *etc.* (see Table 20). The scores for each feature are added to provide a final score whereby the agent is deemed fit or unfit for use in a biocontrol attempt. According to this system, *T. acaciaelongifoliae* would have scored 12 out of 42 points (29%) (Table 20).

TABLE 20 Rating the potential of *T. acaciaelongifoliae as* a biological control agent according to Harris' (1973) system.

Feature	Score	Reason for score
Host specificity	1/3	monophagous
Direct damage	0/5 1/5	gall forming seed reduction of a long-lived perennial
Indirect damage	0/3	none
Phenology of attack	4/4	spans growing season
Number of generations	0/4	univoltine
No. progeny/generation	0/2	<500
Mortality factors	4/4	extensive attack by natural enemies
Feeding behaviour	-	inapplicable
Compatibility with other agents	0/2	agents directly attacking vegetative parts precluded
Distribution	2/6	known to cover 1/2 of native weed range
Evidence of effectiveness	-	irrelevant
Size of agent	0/4	<5mg
TOTAL	12/42 (=28.6%)	

Harris's (1973) system has subsequently been modified by Goeden (1983). Goeden divides the assessment of an agent while it is still in its country of origin into (1) initial assessment of destructiveness in native range and (2) suitability as a biological control agent. He includes a third rating of the potential effectiveness in the area of introduction. This third phase is meant to be done just before, during, or shortly after the introduction and is applicable to species that have been well studied and previously released in other countries. This is irrelevant in the case of ***T. acaciaelongifoliae*** so only the former two phases will be considered here. According to Goeden's system, ***T.***

acaciaelongifoliae is 100% suitable as a biocontrol agent, but still scores only 17 out of 45 (38%) for the assessment of its destructiveness (Table 21). However, it is doubtful whether any researcher would import an agent which is rated ineffective merely because it was suitably specific and easy to culture! This would be especially so if there is a choice of agents, on the same or a different weed species, some of which are difficult to culture but predicted to be more successful.

TABLE 21 Rating the potential of *T. acaciaelongifoliae as* a biological control agent according to Goeden's (1983) system.

Feature	Score	Reason for score
I. INITIAL ASSESSMENT OF DESTRUCTIVENESS IN NATIVE RANGE		
Direct damage	2/6 1/6	gall former seed reduction of a long-lived perennial
Indirect damage	0/6	none
Phenology of attack	6/6	spans growing season
Number of generations	0/3	univoltine
No. progeny/generation	0/3	<500
Mortality factors	6/6	extensive attack by natural enemies
Feeding behaviour	0/3	unknown
Distribution of agent	2/6	known to cover 1/2 of native weed range
TOTAL	17/45 (=37.8%)	

TABLE 21 *continued*

II. SUITABILITY AS A BIOLOGICAL CONTROL AGENT

Host plant source	6/6	obtained from target weed
Ease of culture	4/4	easy
Potential safety	6/6	unreported as pest; no plant pest in same genus or higher taxon
Host-plant specificity	6/6	high
TOTAL	22/22 (=100%)	

It is clear that neither Harris' nor Goeden's approaches would have been suitably predictive in the case of *T. acaciaelongifoliae.* Hokkanen (1985a) concluded that evidence from other successful biocontrol projects also did not support the scoring systems of Harris (1973) and Goeden (1983).

There appear to be no other such systems or approaches which would have been appropriate in the selection of *T. acaciaelongifoliae.* The most recent critique of both Harris' and Goeden's systems is that of Wapshere (1985). Wapshere provides examples of effective agents which would have been incorrectly assessed according to each criterion in Harris' and Goeden's systems. Wapshere ends his critique with the conclusion that the real obstacle preventing the assessment of effectiveness is that one cannot (at this stage) know how much to compensate for parasitism and predation of the agent or competition from other organisms on the same plant. The only guideline he can provide is a practical one of artificially simulating the weed situation within the native range of the plant. The intention is to attract potential agents, and it is recommended that this be done in an area which is eco-climatically most similar to that in the exotic range of the weed. Of course, parasites, predators and competition still complicate the issue. However, artificially simulating the weed situation within the native range of the weed would have been quite impracticable in the case of *T. acaciaelongifoliae* because neither finances nor political realities would allow such a long-term study. *Trichilogaster acaciaelongifoliae* attacks reproductive buds and *A. longifolia* takes three to four years before it becomes fully reproductive.

Recently the most innovative and controversial contribution to the theory of selecting biocontrol agents has been that of Hokkanen & Pimentel (1984) who recommend the selection of agents from plants related to the weed rather than from the weed itself. Because such agents would have a `new' relationship with the host, the possibility of homeostasis is minimised and the agent should be more effective. In contrast, agents with an `old' (evolutionarily long) relationship with their host are more likely to have evolved a degree of homeostasis and thus be less effective. While the control of cacti (Moran *et al.,* 1986) and examples from plant pathology (Hokkanen, 1985b) largely support this view, it has been criticised by Goeden & Kok (1986) and Moran *et al.* (1986). These authors show that many agents, including *T. acaciaelongifoliae,* which have had `long' relationships with their hosts are very effective when freed from their natural enemies. The present project shows that both Hokkanen & Pimentel (1984) and their critics (Goeden & Kok, 1986; Moran *et al.,* 1986) may both be partly incorrect. The truth is that *T. acaciaelongifoliae,* by being released on its host in South Africa in the absence of its natural enemies, does have a 'new' relationship with its host. However, the sense in which *T. acaciaelongifoliae* has a new relationship with *A. longifolia* in South Africa is different to that of Hokkanen & Pimentel (1984) and needs elucidation: In Australia, heavy parasitism and the sparse distribution of *A. longifolia* cause *T. acaciaelongifoliae* to be extremely rare (Neser, 1986). Any homeostasis that may at one time have existed between this insect and its host plant has been lost because the insect never achieves high enough population levels throughout the range of the plant for homeostasis to be selectively maintained. Introducing *T. acaciaelongifoliae is* thus similar to introducing an agent from a related plant species because neither are in homeostatic balance with their hosts. The phenological 'fine tuning' cited by Moran *et al.* (1986) as evidence contrary to Hokkanen & Pimentel (1984) is thus not the reason for the effectiveness of agents such as *T. acaciaelongifoliae.* This phenological fine tuning is merely the result of the old association and many agents which possess this type of fine tuning may be ineffective (see Dennill *et al.,* 1987; Appendix 6). It is in fact the lack of (homeostatic) 'fine tuning' which makes these phenologically finely tuned agents equivalent to Hokkanen & Pimentel's (1986) allegedly more destructive 'new associations'.

Hokkanen & Pimentel (1984) incorrectly assumed that evolutionarily old relationships imply a higher degree of homeostasis. Evolutionarily 'old' relationships can in fact display little or no homeostasis, as in the case of *T. acaciaelongifoliae.* In their criticisms of Hokkanen & Pimentel (1984), Goeden & Kok (1986) and Moran *et al.* (1986) have assumed that the release of the agent from its natural enemies is all

important. This assumption is not necessarily always correct because some evolutionarily old relationships may have some degree of homeostasis which could curtail the effects of the agent even when it released from its natural enemies. For example, the European gall flies released from their natural enemies to control knapweeds in Canada, increased rapidly to reach a population plateau determined ultimately by the plant: the number of galls per seed head was related to the receptacle area of the flower head, apparently because galls which developed earlier in the season did so at the expense of galls developing later (Harris, 1980b). The effects of these gallers were spread throughout the plants (Harris, 1980b) and as many as 21-51% and 6-23% of the heads of diffuse and spotted knapweed, respectively, contained no galls (Harris, 1980c). The seeds escaping attack maintained high knapweed densities (Harris, 1980b). In addition, it has already been mentioned in Chapter 4 that the two gall flies reduced dry weight and seed head production of diffuse knapweed by 71%, whereas no significant reductions in these parameters were achieved by the same flies on spotted knapweed (Harris, 1980b). This is attributed by Harris (1980b) to differences in *host plant phenology*.

The achievement of success in weed biocontrol is essentially dependent on both the release of the agent from its natural enemies *and* **the degree of homeostasis between the plant and the agent. The greater the effect of natural enemies on an agent the country of origin, the less likely the probability of homeostasis between the host plant and the agent; and the more devastating the effects of the agent will be when released on that plant in the absence of its enemies. However, the converse also holds: the less the influence that natural enemies exert on the agent in the country of origin, the greater will be the selection for, and the maintenance of, homeostasis between the host plant and the agent. When such an agent is released on its host plant in the absence of its enemies, its effects on the plant are less likely to be devastating. The issue at stake is not the age of the relationship between the host and the agent, but the degree of homeostasis in the relationship. The biocontrol researcher aims at lack of homeostasis between agent and host, and this can be achieved by using either an 'old' relationship or a 'new' one.**

The most important conclusion to be drawn from the discussion above is that there appears to be an epistemological impasse underlying the issue of predicting the success of agents. The aim of a theory is to achieve predictive, deductive power. However, the theory itself is the product of induction from specific **instances. In weed biocontrol these specific instances are scientific evaluations of the effectiveness of agents** *subsequent* **to release. As Harris** (1980a) has said, the way to improve the effectiveness of biocontrol in the future is to determine what is achieved *by releasing a* certain agent, and then to determine *why.* The dirth of detailed evaluative studies is thus the reason for the theoretical impoverishment in which this science finds itself. It is significant that Wapshere's (1985) critique leaves the researcher largely with his intuition to accommodate for the effects of parasitism, predation and competition. This is no different from the position the biocontrol researcher was in when this science began (see Harris, 1973). Medawar (1969) has shown that intuition is a fundamental and creative element in scientific thinking and as such it should not be feared by the scientist. As more projects are evaluated, the intuitive element in selecting agents will diminish, and a rational, scientific theory should emerge. Hokkanen (1985a) has captured these truths most succinctly:

> "...the chain of events and choices most likely leading to biocontrol success in any project will hardly ever be a dull routine that can be programmed into a computer. it takes experienced, innovative scientists to identify the weak or missing links, and put the pieces of art together, scientifically".

The immediate value of the present project, however, lies in the recommendations for the future selection of agents that can be made as a result of a critical analysis of the features that have contributed to its success.

CRITICAL ANALYSIS OF THE FEATURES THAT HAVE CONTRIBUTED TO THE SUCCESS OF THE PRESENT BIOLOGICAL CONTROL PROJECT

Ecologically important features of the wasp

The following features of *T. acaciaelongifoliae* contributed to the ready establishment and exponential population increases of this wasp.

Trichilogaster acaciaelongifoliae females produce an average of 410 eggs per female. Although Harris (1973) and Goeden (1983) regard an insect producing <500 eggs per female as having a relatively low fecundity, the ability of *T. acaciaelongifoliae* to produce an average of 410 eggs per female (Noble, 1940) has undoubtedly enabled this insect to have a power of increase greater than that of *A. longifolia's rate* of addition of reproductive units. In conjunction with the following two features, this has resulted in

the infestation of 80 and 84% of the branches on *A. longifolia* trees at two study sites within only three generations (Chapter 1; Dennill, 1987 in press; Appendix 2).

The parthenogenesis of *T. acaciaelongifoliae* enables the wasp to utilise its fecundity to full potential. Egg-laying can commence immediately and no time is wasted on mate-finding. This is important in an insect with such a short adult lifespan (mean 2.3 days) (Noble, 1940). Unmated *T. acaciaelongifoliae* females produce females (thelytoky) (Noble, 1940). Chapman (1969) has suggested that the advantage in the evolution of thelytoky is reduced time allocated to mate-finding. This would be particularly advantageous in an insect with as short an adult lifespan as that of *T. acaciaelongifoliae.*

Another advantage of the thelytoky exhibited by *T. acaciaelongifoliae* (Noble, 1940) is that the populations are almost entirely female. This has two beneficial results. Firstly, it greatly increases the reproductive potential of the species (Chapman, 1969). Secondly, since ovipositing females are the actual biocontrol agents, it is beneficial that 84% of the population is of that sex. At present, the sex ratios of *T. acaciaelongifoliae* have been favourable for the control of *A. longifolia.* However, there is no guarantee that these ratios will continue unchanged.

Although *T. acaciaelongifoliae is* mainly thelytokous, it is also able to produce males by normal reproduction. This capacity for normal reproduction removes the only possible disadvantage that the parthenogenesis of *T. acaciaelongifoliae* could have *i.e.* the absence of genetic recombination which could reduce the ability of this species to adapt to environmental changes (Chapman, 1969).

***Trichilogaster acaciaelongifoliae* displays strong, directed flight (Neser, 1985) and can be dispersed passively by wind over long distances. These features have contributed, along with large population size, to the excellent dispersal and establishment of colonies up to 20 km from release points within only three years (Chapter 1; Dennill, 1987 in press; Appendix 2). In addition, *T. acaciaelongifoliae is* able to locate isolated trees and effectively utilise the reproductive buds in all parts of canopies of trees of various shapes and sizes (Chapter 1; Dennill, 1987 in press; Appendix 2).**

Multiple gall formation, which results from a *female T. acaciaelongifoliae* ovipositing more than one egg into a single reproductive bud, is a key feature in the success of this biocontrol programme for two reasons. Firstly, multiple galls produce more wasps per unit dry mass than did single galls and this contributed to the rapid population increases (Chapter 1; Dennill, 1987 in press; Appendix 2). Secondly, multiple galls provide the largest energy sink and contribute indirectly to the loss of a

far greater proportion of inflorescences than the same or even more single-chambered galls would (Chapter 4; Dennill, 1988b in press; Appendix 4).

Lastly, the *T. acaciaelongifoliae* cohorts which were released in South Africa were compatible with the climatic circumstances that *A. longifolia* experiences in the two South African regions in which this weed is most problematic, namely the southern Cape Province and coastal south-western Cape Province (Chapter 5).

Features of the weed

There are three features of *A. longifolia* that have been instrumental in the success of *T. acaciaelongifoliae as* a biocontrol agent. Firstly, except for the inland valleys and west coast of the south-western Cape, *A. longifolia* has invaded regions in South Africa which are the climatic analogues of the areas in which it occurs in its native range. This has facilitated the collection of climatically adapted cohorts of *T. acaciaelongifoliae.* Fortunately, the analogous regions in South Africa include those in which this weed is most invasive. If the exotic range of a weed does not include areas which are climatically analogous to the native range of the weed, this complicates and probably hampers attempts at biocontrol (Goeden, 1983; Hokkanen, 1985a; Huffaker, 1957; Wapshere, 1970b, 1985; Wilson, 1949).

Secondly, the invasiveness *(sensu* reproductive potential) of *A. longifolia* has been overestimated because of the visual impact of the profusion of yellow flowers borne at the onset of reproduction. Milton (1980) expressed surprise to find that *A. longifolia* at her study site produced few pods in relation to flowering efficiency. The present study has shown that *A. longifolia* does not have an endless source of reproductive energy, but that reproduction is a debilitating event which has to be finely balanced with the vegetative growth of the plant. This is mentioned here because *T. acaciaelongifoliae* replaces reproduction in *A. longifolia* with gall formation which is far more energy consuming than the normal reproduction of this plant.

Lastly, the organs which are galled, inflorescences, are produced in large numbers, a high proportion of which are normally abscised if *A. longifolia* is not forced to commit them to gall production.

Features of the interaction between the insect and its host plant

***Trichilogaster acaciaelongifoliae* lives within the tissue which is galled. This ensures that the initiation of galling is perfectly synchronised with the onset of development of the plant organ which is to be galled. Far less impressive seed reduction**

has been achieved by a gall fly that enters the developing seed-heads of knapweed at a more mature stage (Harris, 1980b).

The tissue which is galled by *T. acaciaelongifoliae is* primordial. Galling of primordial tissue is reputed to produce larger and more grotesque galls than galls formed in the more differentiated tissue *e.g.* stem tissue (Ananthakrishnan, 1984). This is due to the plasticity of primordial tissue and the fact that a readily available and rapid nutrient flow towards these tissues is already established and operational at the time required by the gall former. In contrast to *T. acaciaelongifoliae,* the gall fly *Procecidochares utilis* Stone enters its host *Eupatorium adenophorum* Sprengel (Crofton weed) through the primordial tissues of the vegetative buds, but forms galls in the branches and stems. Vegetative growth is not prevented and the impact on the plant is not as spectacular as that of *T. acaciaelongifoliae* on *A. longifolia* (see Julien, 1982).

The phenomenon of 'forced commitment' *i.e.* the ability of the wasp to force its host to mature many more galls than inflorescences, is a key feature of the insect - plant interaction enabling *T. acaciaelongifoliae* to stress *A. longifolia* so effectively in South Africa. The phenology of *T. acaciaelongifoliae* relative to that of *A. longifolia is* such that the reproductive buds are available for oviposition at a stage preceding that at which most abscission of developing inflorescences would occur in the abscence of the galler. This results in forced commitment, and is related to the last point in the preceding section, namely that *A. longifolia* would normally abscise a large proportion of the inflorescences if they were not committed to gall production.

The energy loss caused in *A. longifolia* by *T. acaciaelongifoliae is* the result of (a) the dry mass of the developing galls being so much greater than that of the developing inflorescences and pods, and (b) the fact that the energy content of galls (kj/g dry mass) is not much lower than that of the corresponding plant structures. Ideally, the energy content of the galls should be equal to or greater than that of the normal reproductive structures.

Another critical feature in the success of *T. acaciaelongifoliae is* the fact that gall development spans the entire reproductive and/or growth phase of *A. longifolia.* It is widely regarded that feeding spanning the reproductive/growth phase of the host plant is a key feature of a successful agent *(e.g.* Goeden 1985; Harris, 1973; Hokkanen, 1985a; Wapshere, 1985). Even more important in the present case, however, is that the dry mass of developing galls was relatively greater than that of the developing inflorescences during the earlier part of the reproductive/growth season. This indicates that more stress can be expected than if galling occurred later in the season (Dennill, 1988b in press; Appendix 4; Harris, 1980b; Hartnett & Abrahamson,1979; Maiteki & Lamb, 1985).

Practical features contributing to the success of this project

Collecting the galls in Australia is relatively easy because they are easily detected. Few insects are damaged in transit because they are in the 'dormant' pupal phase which is well protected inside the galls. Because the gall tissue lives for a few weeks after picking, wasps are able to emerge in emergence boxes in quarantine. Very little handling of the insects is thus necessary. The galls are easy to work with and to surface-sterilise in quarantine, and the wasps are not easily damaged. The fact that the gall tissue remains alive for a few weeks after picking also means that the few last instar larvae are provided with their normal food source. No artificial diets or feeding is necessary to sustain any of the insects between exportation from Australia and release in South Africa.

The combined result of these factors was that large numbers of insects were available for initial release (up to 14791). Field releases using local galls were also easily done by merely placing galls in cardboard boxes with two small windows cut out of their sides.

These seemingly mundane considerations should not be underestimated since the difficulty of rearing and releasing insects by artificial means can drastically minimise the chances of successfully establishing them in the new environment (Dennill, 1987; Appendix 5; Dennill *et al.*, 1987; Appendix 6; Mackauer, 1980). Ease of culturing has been included by Goeden (1983) as an important consideration in selecting agents.

Since all of the characteristics listed above may be determined in the country of origin of the weed and the gall former, they can be used as guidelines to select gall forming agents in the future.

SPECIFIC CONTRIBUTIONS' OF THE PRESENT THESIS TO THE THEORY AND PRACTICE OF SELECTING BIOLOGICAL CONTROL AGENTS FOR WEEDS

In terms of their contribution to the knowledge of selecting of biocontrol agents, the features enumerated above fall into three categories : (1) those which are already widely regarded as important, (2) those which confirm characteristics which are tentatively regarded as important, but which require confirmation; and (3) new principles. The high fecundity of *T. acaciaelongifoliae, its* parthenogenesis, excellent ability to disperse, locate and utilise its 'prey' (reproductive buds), its eco-climatic compatibility with the areas in which it was released, and the co-incidence of attack (galling in this case) with the growth or reproductive period of the host, are all universally regarded as key features in a successful biocontrol agent. The present project strongly re-inforces the importance of these attributes.

More interesting, however, are those features which are more tentative and therefore in greater need of confirmation, and those which are completely new. Regarding the former, there are two principles which need discussion. Firstly, the point has already been made that it is generally recognised that agent attack which spans as much of the host plant's growth or reproductive phase is most desirable. However, within the literature on biological control, not much emphasis has been placed on the importance of attack being relatively greater during the earlier part of the growth/reproductive phase of the host plant. This principle has been proposed by ecologists (Hartnett & Abrahamson, 1979) and experimentally demonstrated by pest ecologists (Maiteki & Lamb, 1985). Within the sphere of weed biocontrol, Harris (1980b) has realised the importance of this feature in his analysis of the marked differences in the impact of two gall fly species on knapweeds ; the more damaging species was the one whose galls developed earlier in the reproductive phase of the host plant. The present thesis provides strong confirmation of this principle by showing that the success of *T. acaciaelongifoliae* was largely attributable to the fact that developing galls consumed 3 to 23 times more energy than normal reproduction *during the early part of the host's reproductive and growth phase.* In contrast, mature galls were only three times the energy content of the mature reproductive structures. Secondly, this thesis confirms this principle, from a botanical point of view, by showing how energy consuming reproduction is in the host plant ; *A. longifolia* has to sacrifice growth in order to reproduce, and when this energy expensive activity is replaced by a greater nutrient drainage due to agent attack, the plant is severely debilitated.

Lastly, and most important, are those features of *T. acaciaelongifoliae* and its interaction with *A. longifolia* which provide new and important principles for the future selection of biocontrol agents for weeds. Firstly, although it is widely regarded that parthenogenesis is advantageous in biocontrol agents, the parthenogenesis of *T. acaciaelongifoliae* is especially so because it is thelytokous, which results in a phenomenally high reproductive potential. In contrast to this feature, which is intrinsic to the gall wasp, the other new principles concern the interaction between *T. acaciaelongifoliae* and *A. longifolia.* The first of these is the production of a high proportion of multiple galls which are *(a)* significantly greater in biomass than single galls, pods and stalks, and (b) as productive of *T. acaciaelongifoliae* individuals (per gram biomass) as are single galls. The former causes the immense energy 'sink' which is the key to the success obtained with *T. acaciaelongifoliae* since this energy sink causes the enhanced abscission of ungalled inflorescences on galled trees. The latter contributes to the ecological success (success of establishment) of *T. acaciaelongifoliae* because a high proportion of multiple galls results in a far greater numbers of wasps.

Secondly, *T. acaciaelongifoliae* lives within the tissue which it galls, and this tissue is primordial. These two features ensure (a) that agent attack begins at the onset of the critical growth or reproductive phase of the host plant, and thereby raise the probability that early season attack will be relatively greater than late season attack, and (b) that larger and more grotesque galls (with a greater biomass) can be expected than if the tissue galled was not primordial.

Lastly, forced commitment is a feature that should be sought in potential gall forming agents because of its ability to increase stress load on the host plant. This feature again is a result of the *interaction* between the agent and its host ; it is the result of the (normal) abscission of the organs that would be galled and the fact that galling stops that abscission if those organs are galled. It must be re-emphasised that all of these features can be identified in a potential gall forming biocontrol agent while it is still in its country of origin. These features can therefore be elevated to the logical status of guidelines or principles for the future selection of biocontrol agents for weeds, and as such they may provide important contributions to both the practice and the theory of this science.

In conclusion, the discussion above shows that in addition to confirming the importance of features which are either widely or tentatively regarded as desirable in biocontrol agents, some new and equally important features have been discovered. The discovery of features which contribute to the success of biocontrol agents constitutes the `scientific feedback' which Harris (1980a) regards as an essential [but seldom achieved] aim of biocontrol programmes. It is important to note that all but the first of these new features discussed above have one thing in common, namely that they are aspects of the *interaction* between *T. acaciaelongifoliae* and its host *A. longifolia.* The foundation upon which these principles are based was the detailed quantitative *evaluation* of the effects of *T. acaciaelongifoliae* on *A. longifolia.* That evaluation had two important consequences. Firstly, it showed that gall forming insects can have strong potential in the field of weed biocontrol. Secondly, it provided clues for the examination of the interaction between *T. acaciaelongifoliae* and *A. longifolia* which was necessary in order

to understand *why* this agent is successful. In the field of biological weed control, the lack of detailed evaluation, and its logical successor, the examination of the interaction between agents and their host plants, is echoed in the marked absence of host plant and interaction attributes in the earlier scoring systems of both Harris (1973) and Goeden (1983). The present study has shown, however, that it is the examination of that interaction that has broadened our understanding of some of the features which can contribute to the success of gall forming biocontrol agents.

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SUMMARY

The gall wasp *Trichilogaster acaciaelongifoliae* Froggatt, which galls the reproductive buds of its host plant *Acacia longifolia* (Andr.)Willd, was introduced from Australia to South Africa to reduce the invasiveness of this Australian shrub. The establishment of *T. acaciaelongifoliae,* and its effects on the reproduction and growth of *A. longifolia* under South African conditions are examined. The wasp established readily, populations grew exponentially and the third generation after release had galled 84% and 80% of the branches on trees at two study sites.

Features contributing to the rapid establishment of the wasp include (a) thelytokous parthenogenesis accompanied by a high female to male sex ratio (average 5:1), (b) a high proportion (66%) of multiple galls which produced more insects per gram dry mass of gall tissue than did single galls, (c) negligible parasitism and predation, and (d) efficient location and utilisation of reproductive buds on trees of different shapes and sizes. In addition, strong flight and wind dispersal resulted in establishment of colonies up to 20 km from the large populations at release points after only two generations.

Galling by *T. acaciaelongifoliae* had profound effects on the reproduction and growth of *A. longifolia.* The pod production of trees with >50% of their branches galled was reduced by >89% and >95% at two study sites, irrespective of tree size. Galls caused phyllode abscission, reduced lateral branching by 66% and increased shoot tip mortality to 100% by midsummer. The effects of galling were so severe that the growth and biomass of galled branches was still reduced by *ca* 30% eight months after the galls had desiccated subsequent to adult emergence.

Examination of the phenology of *A. longifolia* and the interaction of *T. acaciaelongifoliae* and this plant explains why the wasp is able to exploit its host so effectively under South African conditions. Reproduction in A. *longifolia* is such an energy consuming process that vegetative growth is sacrificed in order for the plant to have enough resources for reproduction. Phyllode addition during reproduction was strongly inversely related to pod production, both between and, within reproductive seasons. The galling of *T. acaciaelongifoliae* spans the reproductive phase of *A. longifolia* and is far more energy consuming, and this explains why the galling has such detrimental effects on this weed. At various stages of gall development, the biomass of galls was 3 to 25 times that of the normal reproductive structures of *A. longifolia,* and consumed 3 to 23 times more energy than did reproduction in the plant. The large diversion of biomass, and energy, was due to the high proportion of multiple galls produced by *T. acaciaelongifoliae.* The biomass of multiple galls was substantially

greater than that of single galls and pods, whereas the latter two did not differ significantly. Two additional factors contributed substantially to the stress load which *T. acaciaelongifoliae* exerted on *A. longifolia :* (a) the extent of biomass diversion to gall production was relatively greater during the earlier part of the reproductive season, and (b) the wasp sometimes forced the plants to produce up to 200% more galls per branch than the normal quota of inflorescences that the plants were able to produce, a phenomenon called 'forced commitment'. The nett result of all these factors was that galls constituted up to 21% and 40% of the dry and wet above-ground biomass of galled trees respectively, which caused breakage and mortality of large branches and stems during windy periods.

Trichilogaster acaciaelongifoliae* was released at 136 sites throughout the South African distribution of *A. longifolia.* The establishment and subsequent levels of infestation achieved by the wasp were monitored for two to three years. These evaluations show that the wasp established readily and caused high galling intensities in the two regions in which *A. longifolia is* most *invasive,* namely the coastal areas of the south-western and southern Cape Province. However, establishment was poor and levels of infestation declined over three years in the hotter inland valleys and west coast of the south-western Cape Province. Circumstantial evidence indicates that high summer temperatures are limiting the success of the wasp in these areas. The regions from which *T. acaciaelongifoliae* was collected in Australia correspond most closely to those regions in South Africa where the wasp is most successful, and the wasps seem to be ill-adapted to the hot conditions experienced in the abovementioned valleys in South Africa. This information shows that eco-climatic matching may be an important factor determining the success of at least some biocontrol agents, and that *T. acaciaelongifoliae* cohorts from eastern South Australia may establish more successfully in the hotter South African regions invaded by *A. longifolia.

This thesis is placed in context with the literature on gall forming insects, and that for the use of seed reducing agents in biological weed control. The implications of this project for the future control of *A. longifolia* in South Africa are discussed. The key issues in the theory of biological weed control, namely the concept of success and the prediction of success (in selecting biocontrol agents) are critically evaluated in terms of the present project. It is shown that present theory would have been of little use in predicting the outcome of the present project. The usefulness of projects like the present one is shown to lie in the analysis of the features which contributed to its success. These features were attributes of either *(a)* the wasp, (b) the weed, (c) the interaction between the two, or (d) practical features regarding the collection,

transportation, rearing and releasing of the agent. Some of the key features identified in this project merely confirm the importance of attributes already regarded as important. However, other features confirm attributes which have, to date, been tentatively regarded important, and yet others are new additions to this vital aspect of the theory and practice of biological weed control. It is concluded that it is only via the detailed evaluation of the effects of agents on their host plants subsequent to release that one can proceed to the examination of the interaction between agent and host, and that it is only through an understanding of that interaction that the principles for the future selection of agents can be discovered.

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THE EFFECT OF THE GALL WASP *TRICHILOGASTER ACACIAELONGIFOLIAE* (HYMENOPTERA:PTEROMALIDAE) ON REPRODUCTIVE POTENTIAL AND VEGETATIVE GROWTH OF THE WEED *ACACIA LONGIFOLIA*

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ABSTRACT

Dennill, G.B., 1985. The effect of the gall wasp *Trichilogaster acaciaelongifoliae* (Hymenoptera:Pteromalidae) on reproductive potential and vegetative growth of the weed *Acacia longifolia. Agric. Ecosystems Environ.*, 14: 53-61.

The gall wasp, *Trichilogaster acaciaelongifoliae* Froggatt, was introduced from Australia to South Africa for the biological control of *Acacia longifolia* (Andr.) Wild. Comparison of branches from heavily infested trees (those with > 75% of their branches galled) and unifested trees, shows that the gall wasp reduced seed production of A. *longifolia* by 99% and 95% at two sites in the south western Cape Province, South Africa. Seed production of trees was inversely related to the proportion of infested branches and was reduced by an average of 89% when > 50% of the branches on a tree were infested, irrespective of tree size. The seed reduction was achieved directly by galling of reproductive buds and indirectly by increased abscision of inflorescences on galled branches. Galls caused leaf abscision and reduced vegetative growth markedly. The wasps had been present at these sites for only two generations since release.

INTRODUCTION

Acacia longifolia (Andr.) Willd. was imported to South Africa from Australia for dune binding in the early nineteenth century. Since then it has become a major threat to catchment areas, river systems and conservation areas in the south western, southern and south eastern Cape Province (Milton, 1980). This shrub owes its invasiveness largely to its copious production of long-lived seeds (Milton, 1980). The gall wasp *Trichilogaster acaciaelongifoliae* Froggatt was introduced to South Africa from Australia in 1982 and 1983 to reduce seed production of *A. longifolia* (Neser, 1985).

Females of *T. acaciaelongifoliae* lay eggs in the reproductive and vegetative buds of *A. longifolia* causing galls, instead of inflorescences or branches,

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to develop during the following spring. The insect is univoltine although rare bivoltine instances are found (van den Berg, 1979). The biology of the wasp was studied by Noble (1940). Van den Berg (1979) proposed it as a potential biological control agent for *A. longifolia* in South Africa. The wasp was subsequently collected and exported from Australia to South Africa (Neser, 1985) where it was released by the author and Mr. A.J. Gordon. The present study is the first part of an evaluation of this insect as a biological control agent.

METHODS

During December 1981, 217 *T. acaciaelongifoliae* females were caged in gauze sleeves on 21 branches of *A. longifolia* at Vergelegen (i.e., ± 10 females/branch), and 48 females were similarly caged on 10 branches at Banhoek (i.e. t 5 females/branch). Both Vergelegen (17° 56'E;34° 3'S) and Banhoek (17° 58'E;33° 56'S) are situated in the south western Cape Province of South Africa. The climate is mediterranean with 59% of the average 1700 mm rain/year falling during the winter months from May to August. The average temperature for January, the warmest month, is ± 22 °C. The caged wasps were allowed to lay eggs and the gauze sleeves were removed a week later when all the short-lived adults had died. The following year the progeny of the first generation emerged and dispersed naturally.

Evaluation of the gall wasp as a biological control agent began in September 1983 to determine the maximum effect that the insects had on the weed. Branches from infested trees were compared with branches from uninfested trees to determine the effects of galling on inflorescence, pod and seed production and .vegetative growth. The effects of varying intensities of infestation on the seed production of trees was examined.

Since *T. acaciaelongifoliae* was introduced to stop flowering, inflorescence distribution was used as a basis for sampling. About 78% of the

TABLE I

Distribution of the inflorescences on **A. longifolia** branches (based on 60 branches selected randomly from 31 uninfested trees) at Vergelegen in 1983

	Sequential 30-cm branch segment; Tip to trunk			
	1	2	3	4
Number of inflorescences (Total = 2709)	2111	578	20	0.0
Average/segment	35.2	9.6	0.3	0.0
%/segment	77.9	21.3	0.8	0.0

inflorescences on a tree were located in the outer 30 cm segments of the branches (Table I). Unless otherwise stated, the term "branch" is used to signify the outer 30 cm segment of a branch.

Statistical methods and notations used are those of Snedecor and Cochran (1967).

Comparison of inflorescence, pod and seed production of galled and ungalled branches

At Vergelegen, 14 infested trees which displayed the highest levels of infestation were selected. In September, 60 branches with one or more galls were randomly selected and labelled on these trees. Of the sixty branches, 20 were selected at each of three heights viz. 1.0, 1.5 and 2.0 m. Sixty ungalled branches selected similarly from 31 uninfested trees served as controls. Numbers of inflorescences and pods on marked branches were counted monthly. Ripe pods were picked in November and the seeds counted. Similar recordings were made on an additional 23 branches which, although galled, had no galls in their apical 30-cm segments. (Only 23 branches of this type could be found.)

At Banhoek, 40 galled and 40 ungalled branches were similarly selected from 11 infested and 20 uninfested trees, respectively. These branches were used only to compare seed production.

Effect of galling on vegetative growth

For the 60 galled and 60 ungalled branches at Vergelegen, the following were counted: (a) the number of leaves on the original 30 cm segment, (b) the number of nodes and leaves added by apical growth, (c) the number of side shoots added and the total number of leaves added from such growth. The growth tip of each branch was noted as being dead or alive, and the number of individual galls developing on each infested branch was recorded.

Effect of number of galls per branch on (a) inflorescence production and (b) branch tip mortality

At the beginning of this study, 106 galled branches sampled at Vergelegen were used to correlate number of galls per branch with inflorescence production per branch. These branches were grouped into four classes according to number of galls, and the proportion of branches with dead branch tips was calculated for each class.

Effect of galling on pod and seed production of whole trees

Sixteen trees of various sizes displaying various degrees of infestation by the gall wasp were selected at Vergelegen. The number of branches per tree ranged from 33 to 398. The number of galled and ungalled branches were counted on each tree. All the pods were harvested from these trees, not just the pods in the outer 30-cm branch segments, and the seeds were counted. Pod and seed production was corrected to tree size by dividing the number of pods and seeds by the number of branches.

RESULTS

Comparison of inflorescence, pod and seed production of galled and ungalled branches

There was a natural loss of inflorescences. and pods from uninfested branches averaging 63.1% (Table II). However, the loss of inflorescences was much greater on galled branches, leading eventually to a 99.3% reduction in the number of seeds per branch (Table II). The difference in inflorescences per branch at the beginning of the study in September was highly significant (LSD [0.01] =4.0), and increased until final evaluation in mid-November. The average number of seeds per branch (25.9) for the 23 branches with galls internal to their apical 30 cm segments was reduced by 74.2%.

TABLE II

Monthly comparison of inflorescence, pod and seed production of infested *A. longifolia* branches with branches from uninfested trees from September until 17 November 1983 when the pods were picked

		Sept.	Oct.	Nov.	17 Nov.
Inflorescences/ branch	U	35.2	15.7	13.0	13.0
	I	4.4	0.2	0.2	0.2
Pods/branch	U	*	22.0	17.5	16.7
	I	*	0.2	0.2	0.2
Seeds/branch	U				100.3
	I				0.7

U uninfested branches; I = infested branches; * = pods too small to be counted.

At Banhoek, the average number -a seeds per branch was reduced by 95.5% (96.8 and 4.3 seeds per branch for ungalled and galled branches, respectively).

Effect of galling on vegetative growth

There was already a significant reduction of leaves on galled branches of *A. longifolia* in September 1983 (LSD [0.01]=2.0 ; Table HI). The

TABLE III

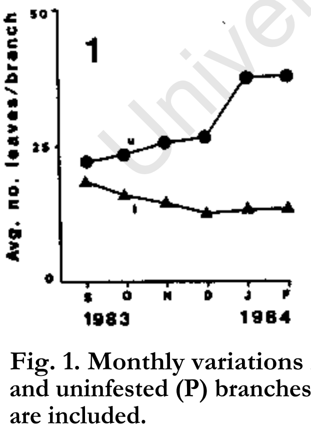
Comparison of the vegetative growth of galled branches and branches from uninfested trees from September 1983 until February 1984

		Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
No. leaves /branch*	U	21.8	21.2	20.6	18.9	—	—
	I	18.3	15.8	14.3	12.6	—	—
No. nodes added/branch apex	U	0.0	0.6	1.2	1.8	2.9	3.4
	I	0.0	0.0	0.0	0.0	0.0	0.0
No. branches added/branch	U	0.0	0.4	0.4	1.6	2.9	3.4
	I	0.0	0.0	0.1	0.1	1.0	1.0

U = uninfested branches; I = infested branches; * = applies to original 30-cm branch only i.e., side-shoots excluded.

number of leaves on ungalled branches increased over the period of study (Fig. 1). This was attributed to addition of leaves to the original 30 cm segments by both apical growth and lateral branching and to a lower incidence of leaf abscision on the original 30 cm segments than on galled branches (Table III). The presence of the galls on infested branches increased leaf abscision on the original 30 cm segment (Table III), increased the incidence of growth tip mortality (Fig. 2) which prevented apical growth and reduced lateral branching (Table III). Galled branches had about half the number of leaves as did the ungalled branches by December 1983. During January and February 1984, delayed lateral branching accounted for a slight increase in leaves on galled branches (Fig. 1, Table III).

Mortality of growth tips on uninfested branches (Fig. 2) results in the



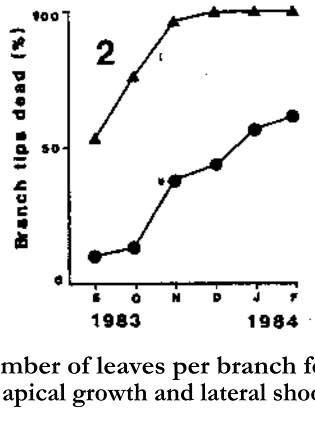


Fig. 1. Monthly variations in the average number of leaves per branch for infested (•) and uninfested (P) branches. Leaves added by apical growth and lateral shoot development are included.

Fig. 2. Monthly variations in the percentage of dead branch tips for infested (•) and uninfested (e) branches.

death of only the one or two apical nodes per branch and differs from tip mortality caused by galling which usually results in the death of a number of nodes per branch.

Effect of number of galls per branch on (a) inflorescence production and (b) branch tip mortality

There was no correlation between number of galls and inflorescences per branch (r^2 and $R^2 = 0.25$) when the study was initiated in September 1983. At that stage, however, there was a significant positive linear trend for the proportion of dead growth tips to vary with the category of gall numbers (***P*** < 0.0001) (Fig. 3). By the time the pods were harvested, branch tip mortality (Fig. 2) and seed production (Table II) were as adversely affected by one as by many galls.

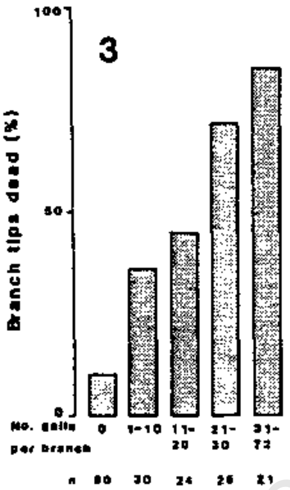


Fig. 3. The effect of varying numbers of galls per branch on branch tip mortality.

Effect of galling on pod and seed production of whole trees

Pod and seed production per branch decreased as percentage infested branches per tree increased (Fig. 4). The average number of seeds per branch for trees with > 50% of their branches galled was 3.6 compared with 31.8 for branches with < 50% of their branches galled. This reduction was statistically significant (LSD [0.05] = 20.7). The lower coefficient of determination for seeds per branch and percentage of branches galled is explained by variation among trees in the number of seeds per pod.

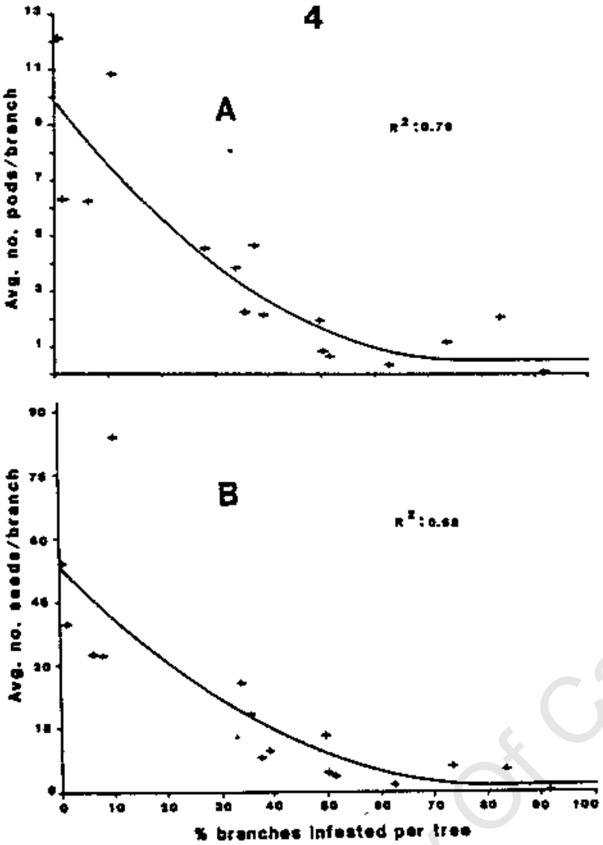


Fig. 4. The effect of varying intensities of gall wasp infestation on (A) pod and (B) seed production of *A. longifolia* trees. The regression equations are Y 9.828 + (-0.243) *X* + (0.002) *X* and Y 53.268 + (-1.281)X + (0.008) *X*, respectively.

DISCUSSION

The results of this study indicate that the gall wasp may dramatically reduce reproductive potential of ***A. longifolia*** trees. The wasp reduced seed production both directly by galling reproductive buds and indirectly by increasing abscision of the remaining inflorescences. The effect of the gall wasp on the 14 selected galled trees at Vergelegen was so marked that whether there was one gall or 72 galls per branch, inflorescence, pod and seed production were equally reduced. This suggested that the proportion of infested branches per tree would be a good measure of the effect of the wasp on pod and seed production. The correlation between the percentage of galled branches and decreased pod and seed production of whole trees confirms both the efficiency of the insect and the method used to demonstrate this.

The shape of the curves illustrated in Fig. 4 indicates that the ***A. longifolia*** plant is unable to compensate for the effects of the insect. The inability of the weed to compensate is partly explained by the loss of leaves and suppression of vegetative growth on galled branches. The large reduction in the number of seeds per branch on the few galled branches whose galls were not located in the outer 30-cm segments is further evidence that the plants are unable to compensate.

Increased abscision of both inflorescences and leaves on galled trees during the first half of summer indicates increased stress on infested plants. The insect is able to impose these indirect effects in addition to direct reduction of seed production for at least three reasons. Firstly, the *wasp* galls the seed-producing structures while they are in physiological contact with the adult plant (as opposed to seed-reducing insects which feed on seeds which are separated from the adult plant). Secondly, the gall *wasp affects* the seed-producing organs throughout their entire period of development. Insects developing in more mature pods or fruits and seeds, even while these are attached to the adult plants, are not likely to act as stress factors sensu Harris (1980) on the adult plants. Lastly, there is the nature of galling itself. Mani (1964) defines galls as pathologically developed cells, tissues or organs of plants that have risen mostly by hypertrophy (abnormally large cell size) and hyperplasy (cell proliferation) under the influence of parasitic organisms. Galling benefits the gall maker and the plant undergoes various injuries including re-directions of growth and sap flow. Flower- or. seed-attacking insects that simply destroy seeds or seed-producing structures without any accompanying physiological and physical distortions in those structures are unable to exert additional stress to the adult plant.

The hakea fruit moth *(Carposina autologa* Meyr.), used to reduce seed production of silky hakea *(Hakea sericca* Schrader) in South Africa, attacks mature seeds when they are completely separated from the parent plant (Neser, 1968, Annecke and Neser, 1977). The weevil *(Erytenna consputa* Pascoe), also used to reduce seed production of silky hakea, attacks 4-week-old fruits (Kluge, 1983). The fruiting organs of the hakea are thus attacked by these insects at a much later stage than those of *A. longifolia* are attacked by the gall *wasp,* and no stress is exerted on the parent hakea tree.

The gall wasps should be able to maintain the levels of infestation found on individual trees in this study, since these results were achieved after only two generations. The 95-99% seed reduction due to *T. acaciaelongifoliae* may be insufficient to stop the weed's dispersal and to reduce the density of the expanding weed population. Harper (1977) cites examples of such failure. However, a 95-99% seed reduction will markedly reduce the rate of spread of any plant (Harper, 1977). The effect of animals, especially birds, which disseminate *A. longifolia seeds,* is unknown at present and will affect the rate of spread of the partially controlled weed. Despite these reservations, if the gall wasp is able to achieve these levels of seed

reduction wherever it is released, it will have fulfilled the purpose for which it was introduced. The gall wasp also appears to be successful by Harris's (1980) criterion which suggests that a biological control agent is successful if it is able to measurably increase the stress load on the target weed.

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Establishment of the Gall Wasp *Trichilogaster Acaciaelongifoliae* (Pteromalidae) for the Biological Control of *Acacia Longifolia* in South Africa

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ABSTRACT

Dennill, G.B., 1987. Establishment of the gall wasp ***Trichilogaster acaciaelongifoliae*** (Pteromalidae) for the biological control of ***Acacia longifolia*** in South Africa. ***Agric. Ecosystems Environ.,*** 19: 000-000.

Trichilogaster acaciaelongifoliae Frogged was introduced to South Africa to reduce seed production of the weed Acacia ***longifolia*** (Andr.)Willd. Population increases and dispersal patterns and rates of the wasp were studied at two sites. Populations increased so dramatically that the third generation after release had infested 84 and 80% of the branches on trees at the two study sites. The wasps had dispersed throughout the 100 x 100-m study sites by two generations after release. The technique for monitoring population increases and pattern of dispersal of the wasp is based on determining the number of branches per tree and percentage of branches galled per tree using basal tree circumference and visual estimations of the proportion of galled branches per tree, respectively. This method is > 90% quicker than counting galled branches, and enables extensive monitoring of the agent. The parthenogenetic, highly fecund female wasps outnumbered males by 5:1. Multiple gall formation contributed to high establishment rates because mulitple galls produce more wasps per unit dry weight of gall tissue than do single galls, and constitute a high proportion (66%) of the galls. Predation and parasitism of the gall wasp are negligible, if the latter occurs at all: the percentage co-emergence of parasitic hymenoptera from galls at five sites over 2 years was 0.1-1.6%. The gall wasp is shown to be very efficient at locating and utilising reproductive buds on trees of different shapes and sizes. This excellent host-seeking ability coupled with wind dispersal and directed flight ***has*** enabled establishment at sites 20 km from release points. All these abilities, in conjunction with the large wasp populations, contribute significantly to the successful dispersal and establishment of this agent. After only three generations since release, the gall wasp has reduced seed production at the two study sites by between 73 and 91%, and 83 and 95%.

INTRODUCTION

Acacia longifolia (Andr.) Willd. was introduced to South Africa from Australia for dune binding in the early nineteenth century (Boucher and Stirton,

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1978). It subsequently invaded river systems, catchments and conservation areas in the southwestern, southern and southeastern Cape Province (Milton, 1980) , and was recently rated the second most important invasive plant in the highly endangered fynbos biome (the Cape Floristic Kingdom) (Macdonald and Jarman, 1984). The invasiveness of this plant is largely because of exceptionally high production of long-lived seeds which accumulate in the soil and are stimulated to germinate by fire (Milton, 1980). The gall wasp *Trichilogaster acaciaelongifoliae* Froggatt was introduced to South Africa from Australia to reduce seed production of *A. longifolia* (Dennill, 1985; Neser, 1986).

T. acaciaelongifoliae is univoltine and rarely bivoltine (van den Berg, 1979). During early summer, females lay eggs in the reproductive and vegetative buds of *A. longifolia* which develop into galls instead of inflorescences or branches during the following spring. Depending on the number of eggs laid per bud, single or multiple-celled (=chambered) galls with one insect per chamber result. *T. acaciaelongifoliae* was proposed as a potential biological control agent for *A. longifolia* in South Africa by van den Berg (1979). Since its release in 1982, *T. acaciaelongifoliae* has markedly reduced the reproductive potential and vegetative growth of *A. longifolia* in South Africa (Dennill, 1985). The aims of the present study were (1) to monitor *T. acaciaelongifoliae* population increases, levels of infestation and seed reductions caused *in Acacia longifolia* populations, (2) to examine the rate and pattern of dispersal of the wasp and its host-seeking abilities and (3) to determine .the reasons for the successful establishment.

METHODS

The study was conducted at five sites in the southwestern Cape Province of South Africa. The climate in the southwestern Cape Province is mediterranean, with 59% of the rain (average 1700 mm per year) falling in the winter months of May to August. The warmest month is January (average 22°C).

The term 'branch' refers to the terminal 0.3-m segment of branch, unless stipulated otherwise. This sampling unit is based on inflorescence distribution (Dennill, 1985) because the gall wasp was introduced to stop flowering. Statistical methods and notations are those of Snedecor and Cochran (1967).

Population increases, increasing infestation levels and dispersal

At both Vergelegen (18°56' E;34 ° 3' S) and Banhoek (18°58' E;33'56' S), a 100 x 100-m area was marked in an *A. longifolia* infestation. Tree density at the two sites ranged from 2 to 20 and 2 to 5 trees 10 m-2 , respectively. Within the plots, *A. longifolia* trees were marked at 10-m intervals on 10 transects which were 10 m apart. The plots were located such that the points where the wasps were released were central. In December 1981, 217 and 48 female *T.*

TABLE I

The number of *Trichilogaster acaciaelongifoliae* adults that emerged from galls on *Acacia longifolia* at Vergelegen and Banhoek for two generations after release in 1981

Site	Year	Adults	Remarks
Vergelegen	1981	205	Released
	1982	2245	1st generation
	1983	> 32 333	2nd generation
Banhoek	1981	48	Released
	1982	235	1st generation
	1983	> 1250	2nd generation

acaciaelongifoliae were caged in gauze sleeves on 21 and 10 branches of A. *longifolia* at Vergelgen and Banhoek, respectively. The sleeves were removed after 7 days when the females, which live for 2.3 days on average (Noble, 1940), had oviposited and died. During subsequent seasons, the wasps were allowed to disperse naturally. During spring 1982, the emergence holes on all galls produced by the caged females were counted, and during the next spring (1983) the number of emergence holes on the galls in the four 10X 10-m quadrats around the release point were counted. Only the four central quadrats were counted, since visual assessments indicated that at least 75% of the total population was located immediately around the release points. At Vergelegen, however, the number of galls in the four central quadrats was too high (42 882) to count the exact number of emergence holes. The percentage emergence in a sample of 765 galls was 75%. This figure was used to estimate the number of wasps that emerged from the galls counted at Vergelegen in 1983.

The rapid increase of the *T. acaciaelongifoliae* populations after 2 years (Table I) necessitated the development of an easier method of estimating levels of infestation, which could also be used to monitor rate and pattern of dispersal of the gall wasp and its effects in stands of *A. longifolia.*

A quick method of estimating the proportion of galled branches per tree was tested. A total of 43 trees of various sizes (ranging from 22 to 5616 branches per tree) and degree of infestation by the gall wasp were selected from Vergelegen, Banhoek and Eerste River (18 ° 51' E;33 ° 56 ' S). Percentage of galled branches per tree was estimated after viewing the tree from all sides. Thereafter, the number of galled and ungalled branches on each tree were counted to calculate the actual percentages of galled branches.

At Vergelegen and Banhoek, the tree trunk circumferences were measured (m) at ground level and branches were counted for 23 and 4 trees, respectively, to determine whether basal tree trunk circumference could be used to estimate number of branches per tree. The number of branches per tree ranged from 22 to 4145.

Visual estimations of the proportion of galled branches on a tree were accu-

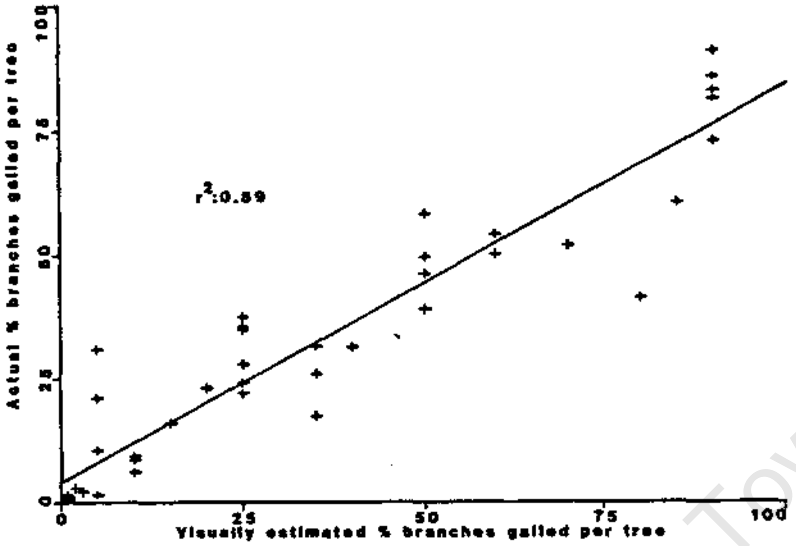


Fig. 1. The relationship between visually estimated and actual percentages of galled branches per *Acacia longifolia* tree ($Y = 4.068 + 0.805X$).

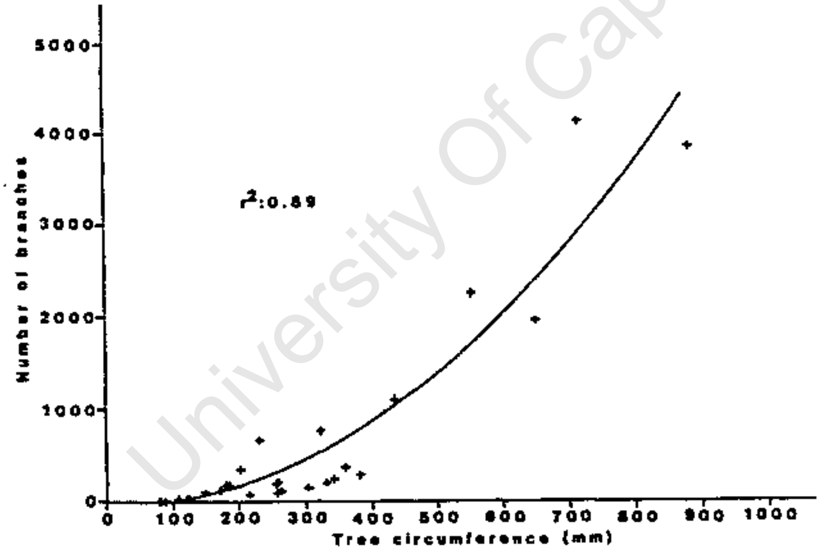


Fig. 2. The relationship between basal tree trunk circumference (mm) and number of branches for *Acacia longifolia* trees at Vergelegen and Banhoek (Y= —83.205+0.006X').

rate when compared with the actual proportions (Fig. 1), and basal tree trunk circumference is a reliable indicator of the number of branches per tree (Fig. 2). These relationships were used to determine (1) the number of galled branches on the marked trees on the plots at Vergelegen and Banhoek, (2) the total number of branches on marked trees and (3) the percentage of galled

branches on each of the marked trees. The annual increase in the number of galled branches at the sites was used as an indicator of population increment. The total number of branches sampled at each site was determined in order to calculate annual increases in the percentage of branches infested by the gall wasp relative to the annual increments in number of branches. The percentage of galled branches in each tree was recorded separately to illustrate visually the increasing levels of infestation and the rate and pattern of dispersal of the wasp.

Extensive estimations of reductions in seed production

At the Vergelegen and Banhoek grids, the number and percentage of marked trees which had 50-75% and > 75% of their branches galled were recorded annually from 1983 to 1985.

The percentage of galled branches per tree can be used as an indicator of seed reduction. Pod and seed production of *A. longifolia* trees is inversely related to the proportion of galled branches on a tree (Dennill, 1985; Dennill, unpublished data). At Vergelegen, pod production of trees with > 50 and > 75% of their branches galled was reduced by 89 and 95%, respectively (Dennill, 1985) . At Eerste River, a riverine site where A. *longifolia* grows into large trees, seed production is reduced by > 95% when as few as 50% of a tree's branches are galled (Dennill, unpublished data) . Thus, one need only determine the number or percentage of sampled trees which have > 50% or > 75% of their branches galled to determine quickly redutions in seed production caused by the gall wasp at a study site.

Number of gall wasps developing per gall

When adult emergence had caused in midsummer 1983,816 galls were sampled at various heights from 20 trees which ranged in galling intensity from 5 to 95% galled branches per tree. These galls were grouped into five classes according to the number of cells per gall. The galls were dried at 60°C for 3 days, and then each gall was weighed and the emergence holes on it counted.

Sex ratios and incidence of parasitism

During October (spring) of 1984 and 1985, galls ($n = 400$ to > 2000) were picked from > 30 trees at each of five sites where the wasp had been released in spring 1981. These sites were Vergelegen, Banhoek, Eerste River, Stellenbosch (18 ° 54' E;33 ° 57' S) and Franschhoek (19 ° 7' E;33 ° 54' S) . The galls were placed in emergence boxes and the number of *T. acaciaelongifoliae* males and females and other insects that emerged were counted. The latter were sent to specialists for identification.

Location and *utilisation of reproductive buds*

At Vergelegen, 1092 infested branches were selected at varying heights on 30 trees in October 1983. The branches were placed in two categories: those with galls in their apical 0.3-m segments and those with galls on the proximal parts of the branch but with no galls on the apical 0.3-m segments.

In October 1984, 100 and 200 infested trees were examined at Eerste River and Vergelegen, respectively. Those trees with noticeable quantities (> 25%) of their infested branches lacking galls in their apical 0.3-m segments were counted.

At Stellenbosch, 100 trees were selected in a dense (1-2 trees m^{-1}) stand of tall A. *longifolia* trees (max. height 7 m) One tree was selected every 5 in on 10 transects which were 5 in apart. Each tree was cut down and divided into 1-m zones above ground level. The numbers of branches and galled branches in each zone were determined.

Gall loss from spring to summer

At Vergelegen and Banhoek, 200 and 100 branches, with one or more galls on them, were marked on 40 and 20 trees, respectively (5 branches per tree) . The galls on each branch were counted at the beginning of September (spring) when the developing galls were clearly visible, and in late November (summer) when the galls were mature.

Correlation of number of cells per gall with decreasing levels of infestation at increasing distances from release point

A series of six groups of six trees was selected at Vergelegen in October 1985. The six trees of the first group were all located within 10 in of the release point and all had about 90% of their branches galled. The second to sixth groups of trees were selected on five hypothetical circles around the release point, such that the trees from the innermost to the outermost circles had approximately 80, 60, 40, 20 and 1% of their branches galled, respectively. The circles were 15 to 20 m apart. Five galled branches were randomly selected at a height of 1-1.5 in from each tree in each group. All the galls were picked off the 30 branches from each group of trees and those galls with one and two cells were counted separately from those with three or more cells.

RESULTS

Population increases, increasing infestation levels and dispersal

The gall wasp populations, which were monitored by estimating the number of galled branches on sampled trees, increased exponentially from 1982 to 1985

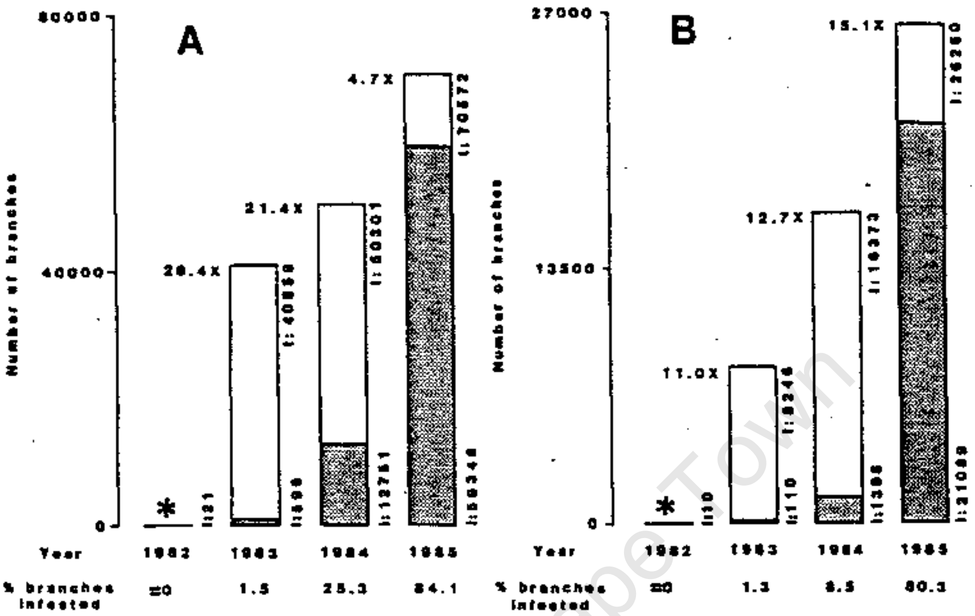


Fig. 3. Annual increase in the total number of branches on sample trees (t), and the number of branches infested (shaded; i) from 1982 (release generation) until 1985 at Vergelegen (A) and Banhoek (B). The multiples whereby the number of infested branches increased annually are indicated by an X and given at the top of each histogram bar.

at Vergelegen and Banhoek (Fig. 3A,B). The percentage of branches infested at both sites also increased similarly, culminating with 84 and 80% of the branches on the Vergelegen and Banhoek plots, respectively, being galled in 1985 (Fig. 3A,B).

In 1983, the highest concentrations of galls were around the release points with light infestations scattered around them (Fig. 4). This pattern changed in 1984 when the infestation levels were somewhat irregular throughout the plots at Vergelegen and Banhoek, and in 1985 when both plots were heavily infested throughout (Fig. 4).

Extensive estimations of reductions in seed production

Within three generations of releasing the gall wasp, the percentages of trees with > 75% and 50-75% of their branches galled were 83 and 95%, and 73 and 91% for Vergelegen and Banhoek, respectively (Table II) . Reductions in seed production at the two sites are thus estimated at 84-95% and 73-91%, respectively.

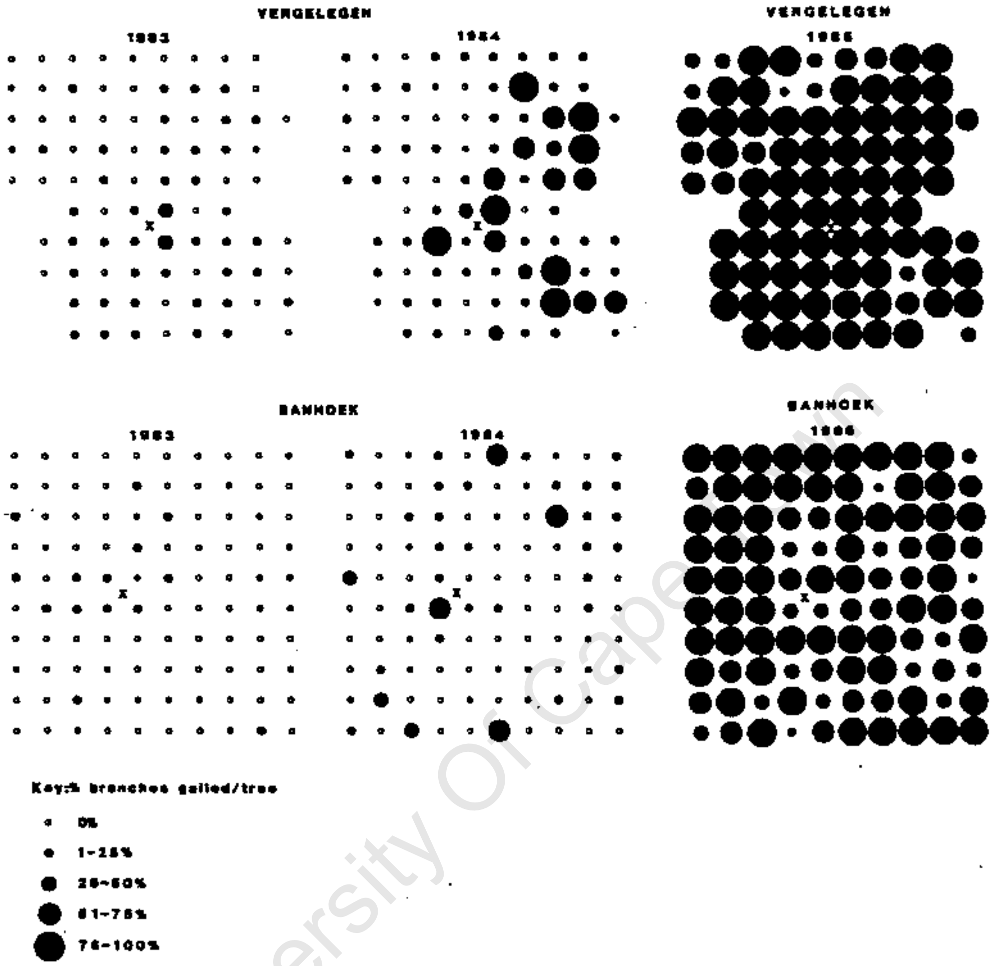


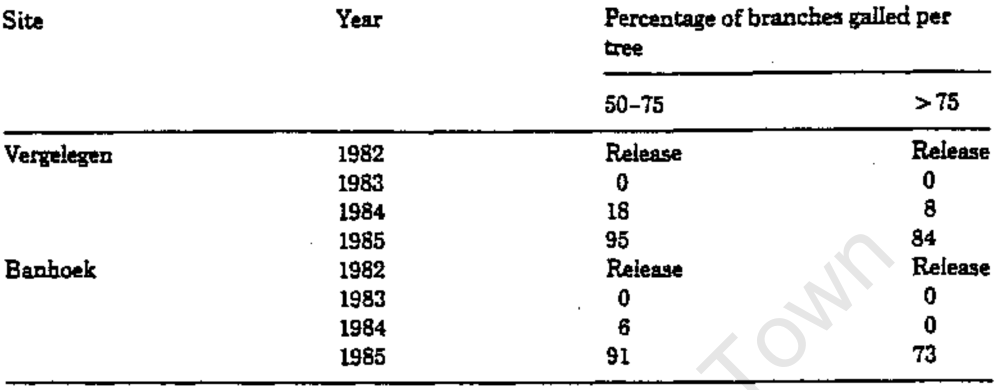
Fig. 4. The rate and pattern of dispersal of *Trichilogaster acaciaelongifoliae* shown by illustrating annual levels of infestation on marked trees on 100 X 100-m plots at Vergelegen and Banhoek from 1983 to 1985 (X = release points).

Number of gall wasps developing per gall

Although there was an overall 24% decrease in the number of insects produced per cell with inreasing number of cells per gall, the number of insects produced per gram of gall dry weight increased by 18% with increasing number of cells (Table III) . The reason for there being an average of 1.1 wasps per cel for single-celled galls (Table III) is the occasional occurrence of a tiny second cell which is externally invisible on a gall which otherwise appears single-celled.

TABLE II

The percentage of sampled A. *longifolia* trees with 50-757o and > *755S* of their branches galled on 100-m² grids at Vergelegen and Banhoek from 1983 to 1985



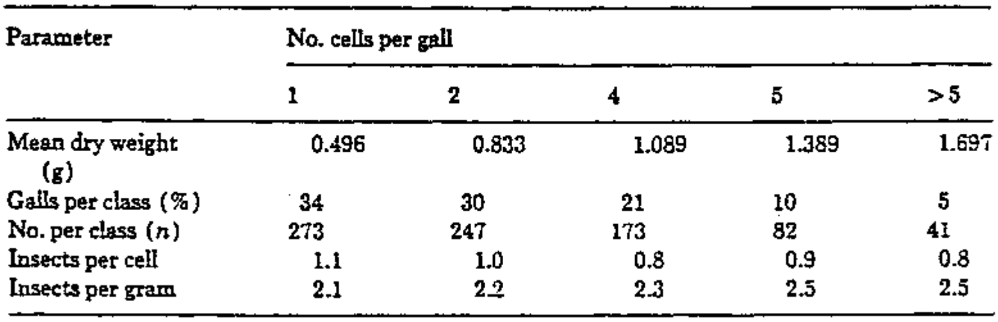
Site	Year	Percentage of branches galled per tree	
		50–75	>75
Vergelegen	1982	Release	Release
	1983	0	0
	1984	18	8
	1985	95	84
Banhoek	1982	Release	Release
	1983	0	0
	1984	6	0
	1985	91	73

Sex ratios and incidence of parasitism

The sex ratio of *T. acaciaelongifoliae* females per male varied between 1.6 and 11.1 but averaged 5.3 for the five sites monitored in 1984 and 1985 (Table IV). The percentage co-emergence of insects other than *T. acaciaelongifoliae* (hymenoptera only) from the galls picked at the five sites that were monitored was consistently low, averaging 0.5% and not exceeding 1.6% (Table IV) . The taxa could be identified only to generic level as *Antistrophoplex* sp. and *Torymus* sp. Although these species are parasitic, it is not known whether they parasitise ***T.*** *acaciaelongifoliae.*

TABLE III

The number of *T. acaciaelongifoliae* maturing per cell and per gram of gall dry weight for galls comprised of varying numbers of cells, and the frequency distribution of the galls composed of different numbers of cells. Tukey's D value (P=0.05) for comparing dry weights of the galls in each class =0.203



Parameter	No. cells per gall				
	1	2	4	5	>5
Mean dry weight (g)	0.496	0.833	1.089	1.389	1.697
Galls per class (%)	34	30	21	10	5
No. per class (*n*)	273	247	173	82	41
Insects per cell	1.1	1.0	0.8	0.9	0.8
Insects per gram	2.1	2.2	2.3	2.5	2.5

TABLE IV

Sex ratios and incidence of co-emergence of other hymenoptera from *T. acaciaelongifoliae* galls picked at five sites in the south western Cape Province

Site	Year	Percentage co-emergence	*n*	Sex ratio
Eerste River	1984	0.1	2088	6.0:1
	1985	0.3	2094	5.8:1
Stellenbosch	1984	0.4	472	1.6:1
	1985	1.6	733	3.5:1
Banhoek	1984	0.5	2000	6.4:1
	1985	0.2	1226	3.6:1
Franschhoek	1984	0.5	2014	11.1:1
	1985	0.1	2142	4.1:1
Vergelegen	1984	0.4	700	6.4:1
	1985	0.9	1346	4.9:1

Location and utilisation of reproductive buds

Of the 1092 infested branches sampled at Vergelegen, only 6.1% did not have galls in their apical 0.3-m segments.

The percentages of the 100 and 200 trees with > 25% of their infested branches lacking galls in their apical 0.3-m segments were only 2 and 3.5% at Eerste River and Vergelegen, respectively.

The distribution of galled branches on *tall A. longifolia* trees at Stellenbosch Mountain was similar to that of the general distribution of branches on the trees (Fig. 5) . There were no galls in the bottom 1-m zone since those branches were all dead.

Gall loss from spring to summer

At Vergelegen, the total number of galls on the sampled branches decreased from 2405 to 2086 (13%), and the mean number of galls per branch decreased slightly from 12 to 10. At Banhoek, the total number of galls decreased from 1450 to 1202 (17%) and the mean number of galls per branch decreased from 14 to 12.7. The loss of developing galls between spring and mid-summer is attributed to branches abrading each other during the excessively windy summer.

Correlation of number of cells per gall with decreasing levels of infestation at increasing distances from release point

There was a significant positive linear trend for the proportion of one- and two-celled galls to increase with decreasing infestation levels at increasing distances from the release point ***(P :5.0.0001)*** (Fig. 6) .

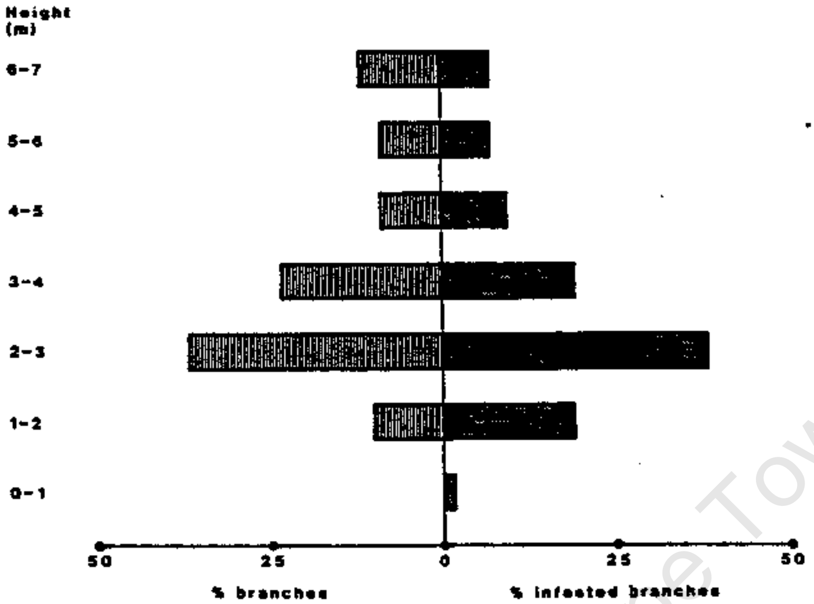


Fig. 5. The vertical distribution of branches in a stand of tall and dense ***Acacia longifolia*** trees at Stellenbosch, and the vertical distribution of galled branches on these trees.

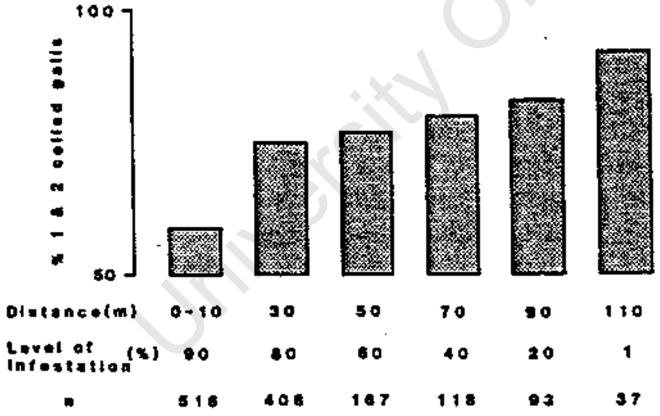


Fig. 6. The relationship between the proportion of one- and two-celled galls with decreasing infestation levels of ***Trichilogaster acaciaelongifoliae*** at increasing distances from the release point at Vergelegen.

DISCUSSION

Basal circumference, diameter or area of tree trunks has been used to estimate size or biomass of forest trees (van Laar and van Lil, 1978), indigenous shrubs (van Wilgen, 1982) and other acacias exotic to South Africa viz. *Acacia*

saligna (Labill.)Wendl. and *Acacia cyclops* A. Cunn. ex G. Don. (Milton, 1980). Using basal circumference of ***A. longifolia*** trees to determine number of branches per tree, and visual estimations of the proportion of galled branches per tree enabled population growth and rate and pattern of dispersal of the gall wasp to be monitored easily and effectively. There is a time saving of > 90% using these methods instead of counting galled and ungalled branches on selected trees.

Evaluations of the effects of seed-reducing biological control agents on weed populations are rarely done (Kluge, 1983; Harley, 1984) , presumably beause of the difficulties of sampling on a large scale. The techniques developed in this study will, however, be very useful for comparing levels of infestation and reductions in pod production at different release sites.

The growth rates of the ***T. acaciaelongifoliae*** populations at Vergelegen and Banhoek were much greater than those of the ***A. longifolia*** trees. This resulted in an increase in the percentage of infested branches and a decrease in pod and seed production which were as impressive as the exponential population increases.

The loss of developing galls between spring and summer when the adult wasps emerge is attributed to the branches abrading each other during the excessively windy summer months. Although as many as 17% of the galls may get broken off the branches, this did not retard the rapid growth of the ***T. acaciaelongifoliae*** populations at Vergelegen and Banhoek. Apart from the gall wasp being introduced without its natural enemies and tie low incidence of parasitism of the weasp in South Africa, there are a number of other important reasons for the phenomenal population growth rates.

Female ***T. acaciaelongifoliae*** are highly fecund. The average number of eggs per newly hatched female is 410 (Noble, 1940) . Despite the short duration of the adult phase (average 2.3 days), the females are parthenogenetic and oviposition can commence immediately (Noble, 1940). No time need be spent locating a mate. In addition, the parthenogenetic females tend to outnumber males. Since the females on their own are the actual biological control agents, it is obviously beneficial that relatively few galls are spent producing males.

The high productivity of multiple-celled galls also contributes to the population growth. Multiple galls constitute about 66% of the galls, and if gall wasp survival rate dereased significantly (e.g. because of competition) with increasing number of cells per gall, this could have a detrimental effect on the population growth of the wasp. In terms of plant material converted into wasps, the multiple-celled ***T. acaciaelongifoliae*** galls are more productive than single-celled galls.

Given an abundance of ***A. longifolia*** buds in which to oviposit, ***T. acaciaelongifoliae*** females tend to lay fewer eggs per bud and per branch as they disperse, thus producing scattered single- and double-celled galls. This behaviour accounts for the initial patterns of dispersal at Vergelegen and Banhoek, in which the highest concentrations of galls were located around the release points. The large populations increased proportionately the rate of dispersal of the wasps, resulting in high infestation levels at points scattered throughout the study sites in 1984 and 1985.

Females that have laid eggs for a few hours begin to fly, especially as daily temperatures increase, and exhibit strong, directed flight (Neser, 1986). In 1984 and 1985, galls were found on trees up to 20 in from release points in the southwestern Cape Province. Wind dispersal is apparently responsible for the large distances covered and, coupled with excellent flying and host-seeking ability, results in successful establishment of remote colonies.

Predation of ***T. acaciaelongifoliae*** by salticid spiders ***(Plexippus*** sp.) and birds is not adversely affecting the wasp populations. The short duration of the period of peak emergence of adult ***T. acaciaelongifoliae*** (<1 month) will limit the increase of such predator populations. Parasitism is negligible if it occurs at alL

Reductions in seed production retard the rate at which any plant spreads (Harper, 1977). The seed reductions caused by ***Trichilogaster acaciaelongifoliae*** will thus markedly retard the dispersal rate of ***Accia longifolia.*** Visual observations at release sites other than those studied here indicate that establishment and levels of infestation are similarly impressive. In addition to the effects of the wasp on reproductive potential, the suppressive effects it has on vegetative growth of ***A. longifolia*** will result in significant and large-scale reductions in biomass of the adult weed populations (Dennill, 1985; Dennill, unpublished data).

These results indicate that ***T. acaciaelongifoliae is*** a successful biological control agent; it is accomplishing very effectively the purpose for which it was introduced (seed reduction) while measurably increasing the stress load on the target weed. The latter alone is regarded by Harris (1980) as a criterion for success of any biologial control agent. Although gall forming insects have seldom been used in biological control programmes, and were initially rated very poorly as potential agents, ***T. acaciaelongifoliae*** exemplifies that at least some gall formers have strong potential for biological control of weeds.

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The importance of understanding host plant phenology in the biological control of *Acacia longifolia**

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SUMMARY

In order to assess the effect of an introduced gall wasp on the weed *Acacia longifolia,* it was necessary to study the vegetative growth and reproductive potential of uninfested trees. The growth of branches on uninfested trees was studied over one year. The results yielded a growth phenology which is notably different from the growth phenology of A. *longifolia* described by Milton (1980). Milton (1980) observed no flushing, but a gradual increase and decline in growth during spring and late summer, repectively. The present study showed distinct flushing, and a marked lack of growth during spring. Examination of the effect of reproduction on the vegetative growth of *A. longifolia* explains the disparity. *A. longifolia* reproduces during spring. Comparison of phyllode addition during spring with pod production for three successive years at one site, and for two years at another, shows that phyllode addition is low during years of high pod production, and *vice versa.* Between trees, phyllode addition is also inversely related to pod production within a reproductive season. Because the present growth phenology was done during a year of high pod production, growth during spring was negligible, in contrast with Milton's (1980) phenology which was done in a year of low pod production and high phyllode addition. Depending on the year in which the plant was studied, its reproductive potential and vegetative growth could have been under- or overestimated by as much as 62% and 90%, respectively. This study shows that the phenology of weeds needs to be examined for at least two years in order not to under- or overestimate their reproductive or growth potential. This is especially important when assessing the efficacy of biological control agents.

INTRODUCTION

***Acacia longifolia* (Andr.) Willd. was introduced from Australia to South Africa for dune binding *ca* 1830 (Boucher & Stirton 1978; Shaughnessy, 1980). In 1984 it was**

rated the second most important invasive alien plant in the endangered fynbos biome (=Cape Floristic Kingdom) (Macdonald & Jarman, 1984). The high production of long-lived seeds which accumulate in the soil has been identified as the main reason for the invasiveness of *A. longifolia* (Milton 1980; Milton & Hall, 1981). The seeds can reach densities of 34000 seeds/m^2 (Pieterse, 1986) and are stimulated to germinate *en masse* by fire. Fire is a feature of fynbos ecology (Van Wilgen, 1982; Kruger & Bigalke, 1984).

In 1982 and 1983, the gall wasp *Trichilogaster acaciaelongifoliae* Froggatt, which galls reproductive buds of *A. longifolia,* was introduced to South Africa from Australia to reduce the seed production of this weed (Dennill, 1985; Neser, 1985). It was shown that in addition to reducing seed production, the wasp also reduces vegetative growth of this weed (Dennill, 1985). In order to demonstrate these effects, the reproductive potential and vegetative growth of uninfested trees needed to be studied as controls. The data presented here were thus obtained.

METHODS

The studies were done at two sites, Vergelegen (18°56'E;34°3'S) and Banhoek River (18°58'E;33°56'S), both of which are situated in the south-western Cape Province. The climate is mediterranean with 59% of the 1700mm rain/yr falling during winter from May to August. January is the warmest month with an average temperature of 22°C. The growth habit of *A. longifolia* at Vergelegen, situated on the foothills of the Hottentot's Holland Mountains, is shrub-like (1 to 4 m high). In contrast, *A. longifolia* grows as a large tree (up to 7 m) on the banks of the Banhoek River which provides a perennial water source.

Statistical methods and notations are those of Snedecor & Cochran (1967). Unless stipulated otherwise, the term "branch" refers to the terminal 30-cm segment of a branch. This sampling unit is based on inflorescence distribution (Dennill, 1985).

Growth phenology

In September 1983, 60 branches were randomly selected on 31 *A. longifolia* trees at Vergelegen. Of the 60 branches, 20 were selected at each of three heights *viz.* 1.0, 1.5 and 2.0 m. From September 1983 until August 1984, monthly counts were made of the phyllodes on the original 30-cm segment, the phyllodes added by apical growth of the 30-cm shoots, and phyllodes added by lateral branching. The number of phyllodes was totalled to provide a monthly index of growth throughout the study period.

Effect of reproduction on vegetative growth

At Vergelegen in 1984 and 1985, 40 and 150 branches were selected on 10 and 30 trees, respectively, in the manner described above. At Banhoek River in 1984 and 1985, 60 and 33 branches were similarly selected on 22 and 20 trees, respectively. For all of these branches, and those selected at Vergelegen in 1983 (see section above), final pod production per branch and the number of phyllodes added during the reproductive period from September to mid-November (when the seeds are dropped), were determined. Independent sets of sample trees were selected randomly each year. All of the trees used were, however, within an area of 100 by 100 m.

The branches marked at Vergelegen in 1984 were selected in such a way that four branches were on each of 10 *A. longifolia* trees. In order to determine the relationship between vegetative growth and pod production within a reproductive season, the number of phyllodes added to each branch over the reproductive period (from September to mid-November) and the number of pods produced per branch were averaged for the branches from each tree.

RESULTS

Growth phenology

Vegetative growth displayed marked flushing ; three periods of active phyllode addition were noted during December, April and July (Fig. 1). During the periods between these flushes, *viz.* late summer and winter, phyllode addition practically ceased. It is particularly noteworthy that growth was also negligible during early summer from September (spring) until December 1983.

Effect of reproduction on vegetative growth

The annual pod production of *A. longifolia* trees at Vergelegen and Banhoek varied markedly between years (Table 1). The results indicate that pod production is cyclical, years of high pod production being followed by years of lower pod production, and *vice versa.* More important, however, is the fact that vegetative growth during spring was markedly reduced during years of higher pod production. This effect was more marked at Vergelegen, a drier non-riverine site than the site at Banhoek River where the trees have a perennial water source.

Table 1. *Phyllode addition* versus *pod production during spring for* A. longifolia *trees at Vergelegen in 1983, 1984 and 1985 and at Banhoek in 1984 and 1985.*

Site & year	No. phyllodes/branch			No. pods / branch		
	Mean	S.E.	d.f.	Mean	S.E.	d.f.
VERGELEGEN						
1983	5.37	1.67	59	16.72	1.25	59
1984	28.58	4.09	39	6.37	1.16	39
1985	2.74	0.69	149	9.91	0.51	149
BANHOEK						
1984	5.37	1.69	59	20.18	1.35	59
1985	9.82	2.77	32	14.36	1.40	32

At Vergelegen, the number of phyllodes added during the reproductive phase was strongly negatively correlated with the number of pods produced per branch during early summer in 1984 (Fig. 2), a year of low pod production at this site (Table 1).

DISCUSSION

The growth phenology of *A. longifolia* from January to August is relatively easy to explain in terms of climate. *A. longifolia* originates from an area of all year rainfall in south-eastern Australia (Costermans, 1981). The cessation of vegetative growth from January to March is thus probably due to the fact that these are the hottest and driest months of the year in the south-western Cape Province. The growth flush observed during April was probably due to the onset of the rainy season coupled with mild temperatures. During May and June, growth again ceased because of low temperatures and short daylength. By the beginning of August, increasing temperatures and daylength, and the availability of rain can explain the growth observed here. Milton (1980) also recorded (a) a secondary growth phase in autumn, (b) minimal growth during winter when monthly temperatures fell below 15 °C and daylength below 7.5 sunlight hours per day and (c) the initiation of growth during late winter.

The growth phenology observed in this study from September 1983 until January 1984 is, however, unrelated to climate ; temperatures are equable, and water availability is high at the tailing off of the rainy season which would have replenished soil-borne water sources. Yet growth was minimal from September until November. In contrast, Milton (1980) recorded the largest growth increments during this period, and that the increment was gradual and steady during early summer (Fig. 3). She emphasised that the increase and subsequent decline in growth of *A. longifolia* during early and late summer, respectively, was gradual and unlike the other alien Australian acacias which displayed distinct flushing. Why, in the present study was there so little growth during this period from September to November, followed a distinct flush during December? My thesis is that I studied the growth phenology of this species during a year of high pod production whereas Milton (1980) studied it during a year of low pod production.

The present studies show clearly that pod production of *A. longifolia* is inversely related to vegetative growth, both within a reproductive season, and between successive seasons. The cost of pod production to *A. longifolia is* so great that even during 1984, a year of low pod production at Vergelegen, the number of phyllodes added during the reproductive phase was strongly inversely related to the number of pods produced per branch. In a year when pod production is high, these pods are produced at the expense of vegetative growth. 1983 was a year of high pod production at Vergelegen (Table 1). This then explains why no growth occurred between September and November in 1983 at Vergelegen (Fig. 1). After pod maturation and seed drop had occurred in November, a growth flush occurred in December before summer temperatures' got too high and water availability too low.

There is also evidence from Milton (1980) to support this hypothesis. I quote Milton on the fruiting success of *A. longifolia* during the same year at the site at which her growth phenology was done: "Although *A. longifolia* generally sets abundant fruit at the University site, yields appear to be chronically low on certain individuals [and on parts of the tree that receive little sun]" (page C15). Regarding another Australian acacia species studied, Milton similarly notes that "The observed poor crop on *A. podalyriifolia* [A. Cunn ex G.Don.] may be due either to environmental factors *or an inherited trait"* (page C15) (my italics). It appears that these alien acacias do indeed have inherent mechanisms determining the allocation of resources between growth and reproduction and that these may be expressed cyclically, subject to prevailing climatic and edaphic factors. Morris (1951) found that balsam fir usually set heavy crops of flowers and seeds every second year, and that the quantity of foliage (number of needles) produced during flowering years was much less than in non-flowering years. He specifically

mentions that the number of needles is determined by the number of primordia produced during the previous season. This suggests that the resources for growth or reproduction are determined in advance. Li (1984) has shown that removing the flower buds of *Paulownia* trees could prevent the consumption of large amounts of nutrients for reproduction and hence increase their volume compared with untreated trees.

The ability of the gall wasp *T. acaciaelongifoliae* to reduce pod production of *A. longifolia* was first studied at Vergelegen in 1983 (Dennill, 1985). Galled branches averaged 0.2 pods as opposed to 16.7 on branches from uninfested trees. If that study had been done at the same site in 1984, when pod production of uninfested trees was lower (6.3 pods/branch), the reduction in pod production due to the wasp would not have been numerically as impressive, and the reproductive and growth potential of the weed could have been under- and overestimated by 62% and 90% respectively.

These studies indicate that caution must be taken not to base phenologies on one year's data. In particular, the biological control researcher must not assess the reproductive or growth potential of a weed in only one year.

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Captions for figures

Fig. 1. The growth phenology of *A. longifolia* from September 1983 until August 1984 at Vergelegen.

Fig. 2. The effect of pod production on spring vegetative growth of *A. longifolia* trees at Vergelegen in 1984. Regression equation Y = 14.418 + 28.444/ X.

Fig. 3. The growth phenology of *A. longifolia* according to Milton (a) (reproduced from Milton (1980)), and a directly comparable phenology based on the data collected in the present study (b). sp = spring, su = summer and au = autumn.

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Why a gall former can be a good biocontrol agent: the gall *wasp Trichilogaster acaciaelongifoliae* and the weed *Acacia longifolia*

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ABSTRACT. 1. The pteromalid *Trichilogaster acaciaelongifoliae* (Froggatt) causes galls to develop in the place of inflorescence during the reproductive phase of its host *A.longifolia* (Andr.) Willd. (Fabaceae). After being introduced to South Africa during 1982 and 1983, this wasp reduced the reproductive potential of *A.longifolia* by >89% when only 50% of the branches on a tree were galled. In addition, vegetation growth of galled branches was reduced by 53% when the vacated galls had desiccated.

2. The wasp is able to manipulate its host so effectively because: (a) the dry mass of developing galls was significantly greater than that of the corresponding reproductive organs peaking in spring (September) when galls were 25 times the mass of unfertilised inflorescences. (b) The large biomass diverted to gall production is accounted for by a high proportion (67-73%) of multiple-chambered galls. The dry mass of multiple-chambered galls was significantly greater than that of both single-chambered galls and pods. (c) The exteut of biomass diversion to gall production was relatively greater during the earlier part of the reproductive season, enhancing stress on the host. (d) The wasp sometimes forced the plant to produce up to 200% more galls per branch than the normal quota of inflorescences. This phenomenon, called forced commitment, further increases stress on the host plant. (e) Galls constituted up to 21% and 40% of the dry and wet biomass of above-ground parts of infested trees, respectively. This caused breakage and mortality of large branches and stems. (1) Reproduction in *A.longifolia* has been shown elsewhere to be so energy consuming that vegetative growth is strongly inversely related to pod production. Because the stress from galling by *T.acaciaelongifoliae* coincides with and replaces reproduction with a greater stress, successful reduction of both reproduction and vegetative growth are achieved.

3. This biological control programme is the first in which a gall-forming hymenopteran has been used to control a weed. Since the effects of gall-formers are indirect compared with those of insects attacking vegetative plant parts, their potential as biocontrol agents has been underrated. This research provides ecologically based guidelines for the future selection of such agents.

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Introduction

Gall-forming insects have seldom been used to control weeds (Julien, 1982; Maw, 1984). Since their effects are indirect compared with those of insects attacking vegetative plant parts. their potential for biocontrol has been underestimated (Harris, 1973). Their high degree of host specificity (Ananthakrishnan, 1984; Dixon, 1983; Mani, 1964) has, however, suited them for the control of alien acacias in South Africa since some of these ***Acacia*** species are grown commercially (Neser & Moran, 1985).

Acacia longifolia (Andr.) Willd. was one of the least widely planted of several Australian plant species introduced to South Africa four dune binding ***c.*** 1830 (Boucher & Stirton. 1978; Shaughnessy, 1980). However, ***A.longifolia*** was recently rated the second most important invasive alien plant in the highly endangered Caper Floristic Kingdom (Cape fynbos) (Macdonald & Jarman, 1984). In South Africa, ***A.longifolia*** invades river systems where it grows as a large tree, but also forms dense thickets of shrub-like plants on mountain slopes away from perennial water. This plant's invasiveness is attributed mainly to a high production of long-lived seeds (Milton & Hall, 1981) which accumulate in the soil up to densities of 34000 seeds m-2 (Pieterse, 1986). Germination of these seeds is stimulated by fire (Pieterse & Cairns, 1986). Fire is both a frequent and necessary phenomenon in fynbos ecology (Kruger & Bigalke, 1984; Van Wilgen , 1982).

The Pteromalid wasp ***Trichilogaster acaciaelon gifoliae*** Froggatt, which galls the reproductive buds of ***Acacia longifolia,*** was proposed as a seed-reducing agent for this weed in 1979 (Van den Berg, 1979). ***T.acaciaelongifoliae*** is univoltine although rare bivoltinism occurs (Van den Berg, 1979). Salient features of the wasp's biology, studied by Noble (1940), are mentioned here. The galls develop during the early southern hemisphere summer from July to November, the time when the plant reproduces and grows (Milton, 1980; Milton & Hall, 1981). Peak emergence of the short-lived adults (average 2.3 days) occurs during November when the pods ripen. The fecund females (average 409 eggs) are parthenogenetic and immediately begin to oviposit in buds destined to become inflorescences or branches during the following spring. Galls composed of one to seven chambers (containing one insect each)

FIG. 1. *Acacia longifolia* trees bearing no pods and showing shoot die-back and loss of phyllodes as a result of heavy galling by the gall wasp *T.acaciaelongilfoliae*.

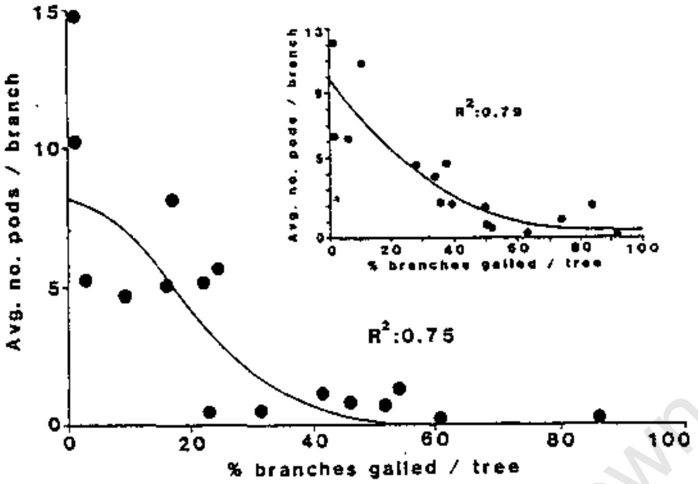


FIG. 2. The effect of varying intensities of gall wasp infestation on pod production of large *A.longifolia* trees at Eerste River (regression equation Y=8.149. e(°"^{40}). The inset illustrates the same relationship for shrub-like trees at a non-riverine site. and is reproduced from Dennill (1985).

Methods: Sixteen trees of various sizes and degrees of infestation by the gall wasp were selected at Eerste River (18.5 1'E; 33˚56'S) in 1984. The number of branches per tree ranged from 136 to 5616 (average 1064). The proportion of branches galled per tree was determined by cutting the tree down and counting galled and ungalled branches. A branch was regarded as galled whether it had one or more galls on it. All the pods were harvested from each tree and pod production was corrected to tree size by dividing the number of pods by the total number of branches per tree.

develop instead of the normal structures from the subsequent July until November. Galling prevents inflorescence development completely, irrespective of the number of chambers per gall.

The wasp was released in South Africa in 1982 and 1983 (Dennill, 1985; Neser, 1985). It established well (e.g. Fig. 1), population increases were exponential and dispersal up to 20 km from release points has been documented (Dennill, 1987b). It was subsequently shown that the seed production of galled trees is inversely related to the proportion of galled branches per tree, irrespective of tree size. Pod production of shrub-like (mountian slope) trees with >50% of their branches galled was reduced by 89% (Dennill, 1985). Pod production of large riverine trees is similarly reduced by >95% (Fig. 2).

The relationship between galling intensity and pod production per tree is non-linear because galling reduces pod production indirectly, by enhancing the abscission of uninfested inflorescences on infested trees, *in addition to* the direct prevention of flowering by gall development (Dennill, 1985). The vegetative growth of the plant is also suppressed by galling. Dennill (1985) measured a 53% reduction in growth of galled branches by the end of gall development. After adult emergence the galls desiccated and the galled trees began to recover. However, the effects of galling were so severe that 30% reductions in number of phyllodes per branch and branch biomass were still significant 8 months after gall desiccation when the galls of the next season began to develop (Dennill, 1987a).

The enhanced abscission of inflorescences, and to a lesser degree, of phyllodes, is the key to the success of this biological control programme obtained so far. Here I report how this is achieved. This paper consists of a number of separate studies with disparate methods. For ease of reading, the methods have been given in the table captions and figure legends.

Results

Energy sink

At various stages of gall development, gall production consumed 3–23 times more energy than reproduction by the host-plant (Figs. 3 and 4).

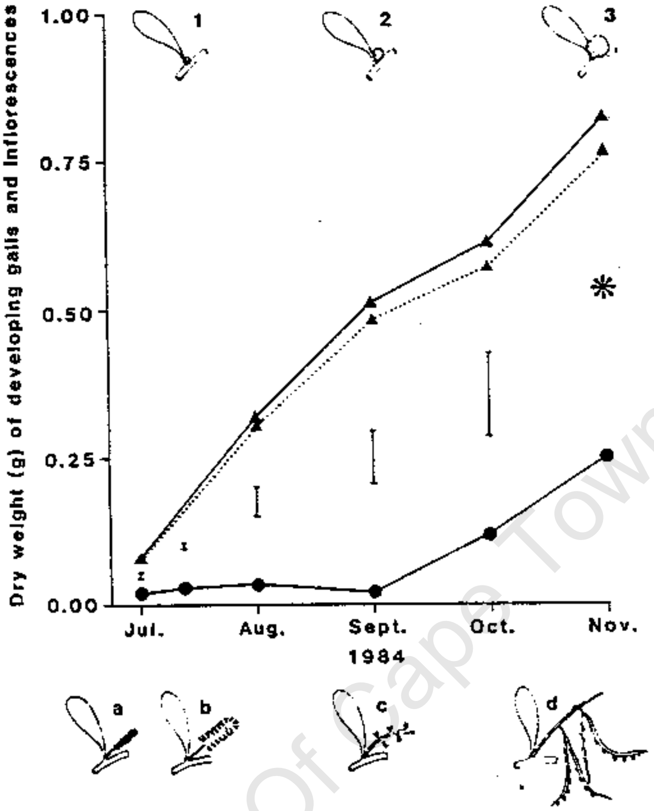


FIG. 3. Monthly comparisons of the dry mass of developing galls (A) and the reproductive organs (•) from July to November 1984 at Vergelegen. The bars represent the I.s.d.s (P=0.05) for the comparisons. The dotted line, which represents nett effective gall biomass, is included since the energy content (kj/g dry mass) of galls was 7% lower than that of normal reproductive tissue (see Fig. 4). 1-3=developing gall; a=unopened inflorescence, b=opened inflorescence, c=opened inflorescence after abscission of unfertilized flowers, d=mature pods. '=instead of comparing dry mass of galls of all sizes with pods in November, these data were treated differently (see Fig. 4). The slight drop in dry mass of the inflorescences in September was due to the abscission of unfertilized flowers.

Methods: From July to November 1984, ten galled branches (with one or more galls/branch) were selected monthly from each of ten randomly chosen infested trees at Vergele„en (18°56'E; 34°3'S). The branches were sampled in equivalent numbers at each of three heights, viz, 1, 1.5 and 2 m on the trees which displayed a range of infestation intensities from 5% to 95% galled branches per tree. Ten branches were similarly selected from ten uninfected trees every month. The developing galls and the reproductive structures were removed from the galled and ungalled branches, respectively. The dry weights of the galls and the inflorescences were determined after drying them at 60°C for 3 days. Because the developing inflorescences were light, the combined weight for all the inflorescences on each of the 100 ungalled branches was determined and divided by the number of inflorescences weighed. The number of replicates for each average weight thus obtained was therefore at least 100. The number of galls used to obtain an average dry weight per gall for each month varied from 97 to 145 (average 119).

Effect of multiple galls

The cost of production of single-chambered galls was not greater than that of pods, but multi-chambered galls were significantly more energy consuming than the former (Fig. 5). The high proportion (66–73%) of multiple galls thus accounts for the large amount of energy diverted to gall production.

Coincidence of galling and host plant reproduction

Galling not only spanned the reproductive phase of *A.longifolia*, but energy diversion to

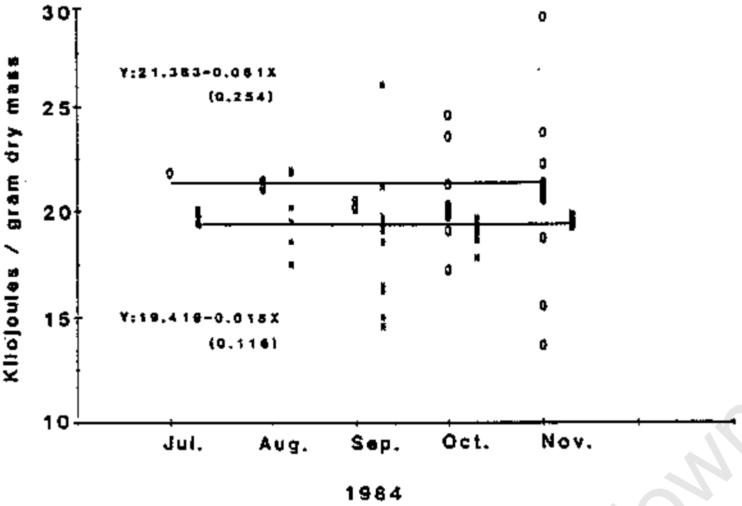


FIG. 4. The energy content (kj/g dry mass) of developing galls (1 and the reproductive organs (0). The regression coefficients (for slope) did not differ significantly from each other (P>0.50) or zero (P=0.88 and 0.54). but the Y intercepts differed significantly (P<0.001), indicating that the energy content of galls is 6.8% lower than that of the normal reproductive structures throughout their development.

Methods: The monthly samples of developing galls and inflorescences collected from July until November 1984 at Vergelegen (see Fig. 3) were ground, and their energy content determined (kj/g dry mass) using an Auto Bomb Calorimeter.

gall production was greatest during the early part of the reproductive season from July to September when gall dry mass increased rapidly from 4 to 25 times that of fertilized inflorescences (Fig. 3).

Forced commitment

The wasp sometimes committed the plants to the production of up to 200% more galls per branch than the normal quota of inflorescences produced by the plants (Table 1). This phenomenon, which I term *forced commitment*, can greatly increase stress on the weed.

Above-ground biomass composed of galls

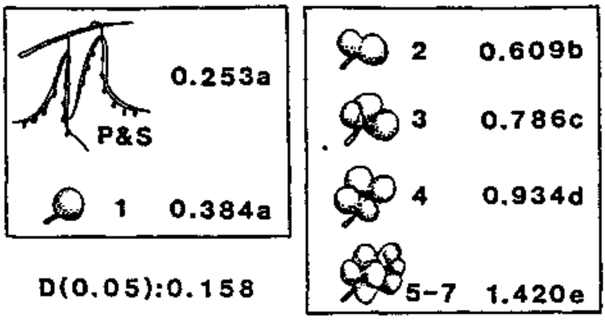
Galls constituted up to 21% and 40% of the dry and wet above-ground biomass of infested *A.longifolia* trees, respectively (Table 2).

Discussion

The earlier the initiation of gall development during the reproductive/growth season of a plant, the greater the effect the galler will have on biomass allocations within the plant. This has been suggested for gall formers (Hartnett & Abrahamson, 1979), demonstrated *aposteriori* for gall flies (Harris, 1980a), and experimentally shown for aphids (Maiteki & Lamb, 1985). Aphid feeding acts as a nutrient sink just as galling does.

In the case of *T.acaciaelongifoliae*, gall development is initiated at the onset of inflorescence development, and the biomass and energy diverted to gall production is consequently great. This immediate response to the cues initiating inflorescence development is possible because the insect lives within the reproductive tissues of its host. Moreover, *foliae* galls primordial tissue which is reputed to produce larger and more grotesque galls than galls formed in more differentiated tissue, e.g. stem tissue (Ananthakrishnan, 1984). This is due to the plasticity of the former and the fact that a readily available and rapid nutrient flow towards these tissues is already established and operational at the time required by the gall former.

Multiple-gall production by *T.acaciaelongifoliae* can be viewed as a wastage of eggs, since single-chambered galls stop pod production as effectively as multiple-chambered galls do. However, this inefficiency of the wasp results in



Class	n	%
P&S	102	—
1	281	27(34)
2	231	73(66)
3	233	
4	126	
5-7	162	

FIG. 5. Comparison of the dry weights (grams) of mature pods and their stalks (P & S) with the dry weights of mature galls composed of varying numbers of chambers in November 1984 at Vergelegen. Average dry weights followed by the same letter do not differ significantly whereas those followed by different letters do. The frequency of multiple-chambered galls is shown, and that for another sample of galls is given in parantheses.

Methods: In mid-November when the pods were ripe, a large sample of galls (1033) was collected from at least twenty trees displaying the entire range of galling intensities (1-95% galled branches/tree). Instead of comparing the average dry weight of all the galls with that of the pods and their stalks, the galls were separated into classes according to the number of chambers per gall. The dry weights of the galls in these classes were compared with each other and with the dry weights of ripe pods and their stalks. The proportion of multiple-chambered galls was recorded for this sample of galls, and for another sample of 816 galls similarly picked at Vergelegen in 1984.

the high proportion of multiple galls which in turn causes the relationship between galling intensity and pod production per tree to be non-linear. If only single-chambered galls were produced, far less stress would be exerted on *A.longifolia* trees. There would consequently be much less inflorescence (and phyllode) abscission, the reduction in pod production would be more linearly related to galling intensity, and much higher levels of galling than 50% galled branches per tree would be necessary to reduce pod production by 89–95%.

Forced commitment is the result of the reproductive phenology *A.longifolia*. This plant produces an excess of reproductive buds during spring, which results in an excessive production of inflorescences during the subsequent spring. Many of these are abscised and the number which mature to produce pods depends on intrinsic annual variations and prevailing climatic and edaphic conditions (Dennill, 1988). This is characteristic of Australian acacias (Harley, 1985) and regarded as a strategy of higher plants to ensure reproduction (Addicot, 1982; Harley, 1985). In the present case the full quota of buds are available for oviposition by the wasp during the spring *preceding* that during which abscission of the excess inflorescences occurs. The galls cannot be abscised as the unwanted inflorescences can, and the plant can thus be committed to the production of many more galls than the number of inflorescences it was able to mature at the time.

The cost of reproduction in *A.longifolia* is so great that vegetative growth is strongly inversely related to pod production, both between subsequent reproductive seasons and within a particular reproductive season (Dennill, 1988). When

TABLE 1. Comparison of the number of galls and inflorescences per branch surviving to maturity on infested and uninfested trees, respectively, at Vergelegen and Banhoek River in 1984 and 1985.

Site	Year	Inflorescences per branch	No. galls per branch	l.s.d. (P=0.05)
Vergelegen	1984	4.08	11.73	2.43
Vergelegen	1985	7.78	10.43	1.09
Banhoek River	1984	13.54	9.42	2.15
Banhoek River	1985	10.18	12.65	2.13

Methods: During spring (September) 1985, 200 branches with one or more galls/branch were labelled on forty infested trees at Vergelegen, and 100 galled branches were labelled on twenty infested trees at Banhoek River (i.e. 5 branches/tree). Although these trees were randomly selected, all had more than 75% of their branches galled because levels of infestation were so high at both sites (Dennill, 1987b). As controls, 150 and thirty-three branches were similarly marked on thirty and six uninfested trees at Vergelegen and Banhoek respectively. Fewer ungalled branches were obtained than galled branches at both sites because of the scarcity of uninfested trees, especially at Banhoek River. In mid-November the inflorescences that survived to produce pods on the ungalled branches, and the galls that matured on the galled branches, were counted. The same data had been collected for forty and sixty pairs of galled and ungalled branches at Vergelegen and Banhoek River in 1984. The final production of galls and inflorescences per branch on infested and uninfested plants, respectively, could thus be compared for both sites in 1984 and 1985.

galling coincides with and largely replaces the already costly process of reproduction, this has profound effects on the growth of the plants. Apart from the physiological energy drainage, the high above-ground biomass composed of galls can also cause mechanical breakage of branches, especially during wind.

T.acaciaelongifoliae is presently regarded as an effective agent in the sense that it is achieving the aim for which it was introduced, seed reduction, while also measureably increasing stress on the weed (reducing biomass). The latter alone is regarded by some researchers (Harris, 1980b) as a criterion for success.

Implications

The present studies show clearly that gall-forming insects can have strong potential for the bio-

TABLE 2. The proportion of the wet and dry above-ground biomass of infested *A.longifolia* trees composed of galls at Vergelegen in 1985.

Tree	Wet mass (kg)			Dry mass (kg)		
	Galls	Remainder	%	Galls	Remainder	%
1	5.96	23.93	19.94	1.44	13.73	9.49
2	7.63	12.95	36.24	1.53	7.05	17.78
3	5.26	8.04	39.55	1.23	4.64	20.95
4	1.18	3.70	24.18	0.33	2.00	14.16
5	11.86	28.04	29.70	2.46	15.09	14.02

Methods: Five infested trees of various sizes, ranging from 186 to 1129 branches/tree, and with >75% of their branches galled (ranging from 75.2% to 89.4% branches galled/tree), were cut down at ground level at Vergelegen in November 1985. The galls were removed from each tree and both the wet and dry weights of the galls and of the remainder of each tree were obtained. Although these data were obtained from heavily galled trees, it has been shown that within three generations since release of the wasp, 84% and 73% of the trees at two sites were heavily galled, i.e. having >75% of their branches infested (Dennill, 1987b).

logical control of weeds, and provide the following criteria as guidelines for obtaining success:

1. The agent must live within the tissue which is galled. This ensures that the initiation of galling is perfectly synchronized with the onset of development of the plant organ which is to be galled. Far less impressive seed reduction has been achieved by a gall fly that enters the developing seed-heads of knapweed at a more mature stage (Harris, 1980a).
2. The tissue which is galled should be primordial. In contrast to the present case, the gall fly *Procecidochares utilis* Stone enters its host *Eupatorium adenophorum* Sprengel (Croften weed) through the primordial tissues of the vegetative buds, but forms galls in the branches and stems. Vegetative growth is not prevented and control has been only partial (Julien, 1982).
3. The organs to be galled must be produced in large numbers, a high proportion of which would normally be abscised if the gall former did not commit them to gall production.
4. The dry mass of the developing galls must be substantially greater than that of the corresponding plant structures and their energy content not much lower. Ideally, the energy content of the galls should be equal to or greater than that of the normal reproductive structures.
5. Gall development must span the entire reproductive and/or growth phase.
6. The dry mass of developing galls must be relatively greater during the earlier part of the reproductive/growth season. This indicates that more stress can be expected than if galling occurred later in the season.

Since these characteristics are able to be determined in the country of origin of the weed and the gall former, they can be used to select gall forming agents in the future.

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The importance of technique in establishing biocontrol agents — the moth *Carposina autologa* on *Hakea sericea*

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SUMMARY

The seed attacking moth *Carposina autologa* was released in South Africa for control of the weed *Hakea sericea* but established poorly. Altering the release method such that it corresponded more closely to natural infestation and. better training and supervision of field workers resulted in a 111% increase in success of a subsequent release.

INTRODUCTION

The hakea fruit moth has been introduced from Australia to the Republic of South Africa to reduce the seed production of the the weed *Hakea sericea* Schrader (Neser & Annecke, 1973; Annecke & Neser, 1977). The life cycle and phenology of the insect in Australia have been described by Neser (1968). The fertilised female lays eggs singly or in groups in crevices on the fruits. The hakea fruit consists of two woody halves encapsulating two winged seeds (Fig. 1). The newly hatched *Carposina autologa* larva burrows to the seed cavity from a point on the suture between the two halves of the fruit (Fig. la). Soon after beginning to eat the seeds the larvae begin the exit tunnel, feeding thereafter being interspersed with burrowing until the mature larva falls from the fruit to pupate in the soil.

Since 1972 the moth has been released in South Africa in a number of ways. Firstly, imported surface-sterilised eggs on a small piece of the woody fruit to which they had originally been attached, were stuck onto fruits using paper glue. Subsequently, recently hatched larvae were put onto fruits in the field and adults reared artificially from imported eggs were released. Finally, recently hatched larvae were placed individually into holes drilled into fruits using a portable dental drill.

Using this last technique, developed by Dr B. Gunn of the Plant Protection Research Institute, Stellenbosch, the larvae were placed in 0.5 mm diam. holes drilled 2.0 to 5.0 mm into the suture between the woody halves of the fruit. These larvae were reared from imported eggs and raised on an artificial medium in which each larva was kept separate to avoid cannibalism by placing a short straw over it in the medium. In the field, the medium containing each individual larva was pushed out of its straw. The larva was picked up using a fine paint brush and put into the hole drilled into the fruit. After the larva had crawled into the hole, the hole was sealed with a wax plug to prevent the larva crawling out and to prevent it being attacked by mites.

The present study was undertaken in 1981 (a) to measure the effectiveness of the release method described above, (b) to analyse the factors affecting establishment by this technique and (c) to compare the routes taken by larvae entering and leaving artificially infested fruits in South Africa with those of the larvae infesting fruits naturally in Australia. Subsequently, the success of a technique modified to incorporate these findings was evaluated.

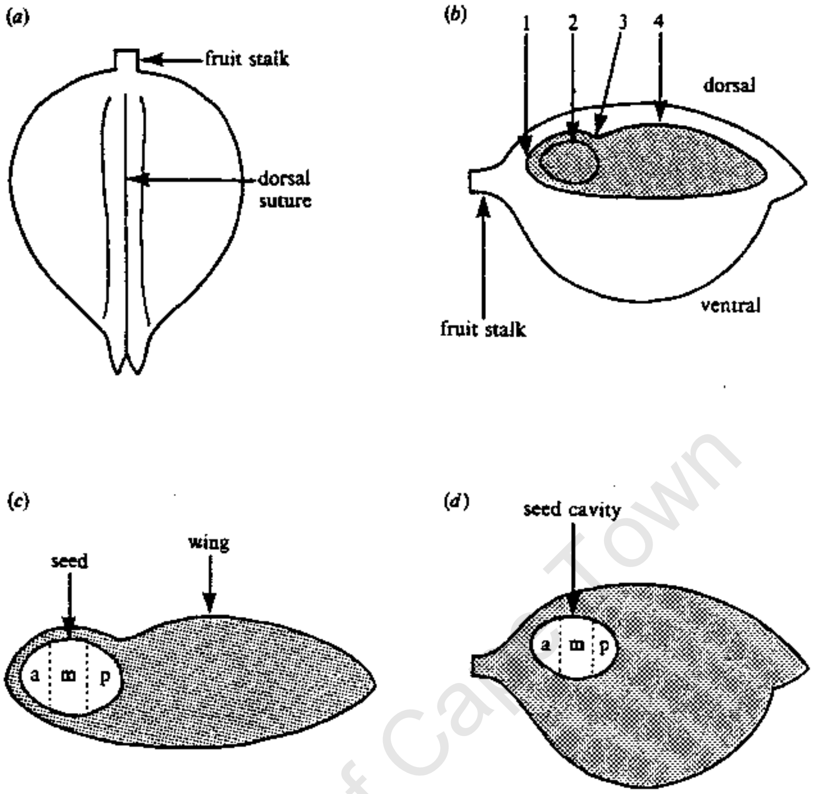

Fig. 1. Diagrams representing *(a)* the dorsal view of a *Hakea sericea* fruit, *(b) a* longitudinal section of a *H. sericea* fruit split along the suture to show the four drilling positions (1, 2, 3 and 4), *(c)* a lateral view of a *H. sericea* seed showing the zones on its surface (a = anterior; m = middle; p = posterior) and *(d) the lateral* view of a *H. sericea* fruit to show the zones on the seed cavity where the *C. Autologa* larvae began their exit routes.

METHODS

Evaluation of existing release method

From March to July 1980, the drilling technique was used to place approximately 1000 larvae individually into fruits on 12 trees. The holes were drilled into the suture between the two halves of the fruits. In June 1981, 991 of the artificially infested fruits were recovered from the field. The recovered fruits from each tree on which larvae were released were kept separate and treated as separate groups (replicates) so that the data could be treated statistically. The fruits thus fell into 12 such replicate groups. The average number of fruits per group was 72, and ranged from 28 to 141. The fruits in each group were divided into two categories, those with emergence holes (successful development to the pupal phase) and those without emergence holes (failures). At this stage the positions of the drilled holes relative to the seed cavities of the fruits were not known.

Each fruit was dissected and microscopically examined. For fruits with emergence holes, the following were determined: (a) the field worker who infested the fruit (the fruits of each worker were marked with a different colour), (b) the position of the drilled hole relative to the seeds (four positions are distinguished in Fig. lb), (c) the zone on the seed surface in which the seed was penetrated (these zones are delimited in Fig. lc) and (d) the zone on the surface of the seed cavity in which the exit burrow left the seed cavity (Fig. 1c/). For fruits without emergence holes, the following information was recorded: (a) the worker who infested the fruit, (b) the

position of the drilled hole and (c) the stage of larval development at which the larva died (these stages are distinguished in the legend to Table 4).

Examination of naturally infested fruits from Australia

Two hundred and seventy Australian fruits with emergence holes (indicating successful development to the pupal phase) were dissected and treated as were the fruits described above. The routes taken by the larvae in penetrating the seed cavities from the suture were categorised as corresponding to drilling posititons 1, 2, 3 or 4 (Fig. lb). These successful natural infestations were compared with the successful artificial infestations made in South Africa in 1980.

Evaluation of the modified release method

The evaluation described above led to the releasing method being modified by using only drilling positions 2 and 3. During the winter of 1981, approximately 1100 fruits were infested on 17 trees by the same three field workers. In June 1982, 1085 of these fruits were recovered from the field. The recovered fruit from the 17 trees fell into 17 groups (replicates). The success of this release was evaluated in the same way as that of the 1980 release.

Data analysis

The data were recorded as percentages. Where comparisons were made, the data were transformed by using working logits, and analyses of variance performed on the transformed data. Statistical notations are those of Snedecor & Cochran (1967).

RESULTS

Evaluation of existing release method

The mean success of the 1980 release was 31% (Table 1). Worker 1 was significantly more successful in infesting fruit than workers 2 and 3 (Table 2). However, worker 1 treated only 19.1% of the total number of fruits. Significantly more establishment resulted by placing larvae in the drilled holes which entered the seed cavity in positions 1, 2 and 3 than in the blind

Table 1. *The mean % of* **Carposina autologa** *larvae which successfully developed to the pupal phase in 1980 and 1981 using the original and modified release methods respectively (D.F. = 20)*

	1980	1981	S.E.D.
Mean % success	30·68	64·74	
Logit	(−0·7672)	(0·6790)	(0·2919)
No. of replicates	12	17	
Mean no. fruits/replicate	82·6	63·8	

Table 2. *The levels of success obtained by three field workers for the 1980 and 1981 releases*

	1980			1981		
Worker	% successes	Logit	n	% successes	Logit	n
1	49·9	(−0·0053)	8	70·1	(0·8568)	14
2	29·4	(−0·9443)	10	63·8	(0·6064)	10
3	17·2	(−1·9914)	5	59·3	(0·3994)	15
S.E.		(0·9190)			(0·8110)	
D.F.		20			36	
Mean no. fruits/ replicate (n)		29			29	

Table 3. *The success of those methods with the drilled hole entering the seed cavity (drilling positions 1, 2 and 3) with those not entering the seed cavity (position 4). 1980 release only.* *D.F. = 24*

Drilling position	No. of replicates	Mean no. fruits /replicate	Mean success		% of total no. fruits (=991) infested
			%	Logit	
1, 2 and 3	18	32·5	58·3	(0·7578)	59·0
4	8	42·3	14·4	(−2·0228)	34·1
Undetermined					6·9
S.E.D.				(0·8328)	

Table 4. *The percentage of mortality at the various stages of penetrating and leaving the fruits for the 1980 and 1981 releases. Stage 1 = squashed by wax plug; 2 = died in drilled hole without making any attempt to burrow further or enter the seeds, 3 = died on testa or on surface of seed cavity; 4 = died between seeds (in most cases the seeds are penetrated on their inner flat surfaces); 5 = died after eating part or all of one or more seeds and had begun exit burrow; 6 = died after burrowing unsuccessfully towards the seed cavity from the drilled hole (for fruits drilled into using position 4) and 7 = died because hole was drilled off the suture*

Stage	% of total mortality	
	1980	1981
1	5·7	4·1
2	32·8	13·1
3	13·1	13·1
4	8·7	12·6
5	4·0	10·8
6	11·6	32·4
7	15·3	1·6
Undetermined	8·7	12·2
Total no. of fruits	687	442

ending holes of drilling position 4 (Table 3). However, a large percentage of fruits had been infested using drilling position 4 (Table 3), diminishing the mean success disproportionately. There was a relatively high percentage mortality (38.5%) at the early stages 1 and 2 than at the later stages 5 and 6 (15.6%) (Table 4).

Examination of naturally infested fruits from Australia

Examination of the Australian fruits showed that a low percentage of larvae (13.3%) entered the seed cavity by a route corresponding to drilling position 4; most larvae entered via a route approximating drilling position 2 (Table 5). The larvae in the Australian fruits and the fruits of both South African releases had a marked preference for entering the seeds in the posterior zones (Table 6).

Evaluation of the modified release method

The mean success of the 1981 release using the modified technique was 65% (Table 1), a statistically significant 111% increase in success compared with the 1980 release (Table 1). The success rates of workers 2 and 3 increased markedly compared with the previous year and there was no statistical difference between the efficiency of the three workers (Table 2). The percentage mortality of larvae at the early stages (stages 1 and 2) was low (17.2%) compared with that at the later stages 5 and 6 (43.2%) (Table 4).

Table 5. *The percentage of larvae entering the seed cavity of naturally infested fruits from Australia via a route comparable with drilling positions 1, 2, 3 and 4 (eight replicates; 25 fruits' replicate)*

	Position of penetration of seed cavity				
	1	2	3	4	S.E.D.
Mean %	11·7	51·7	23·3	13·3	
Logit	(−2·0952)	(0·0636)	(−1·1832)	(−1·9367)	(0·3331)

Table 6. *The mean percentage of larvae entering the seeds in each zone and leaving the seed cavities in each zone for the Australian fruits, and the fruits of the 1980 and 1981 releases in South Africa. These data applies only to fruits with emergence holes (a = anterior; m = middle; p = posterior zones)*

	Avg. % entering in each zone			Avg. % leaving in each zone		
Year/Origin	a	m	p	a	m	p
Australian fruits	1·4 ± 3·9	3·4 ± 5·5	95·2 ± 5·9	7·6 ± 7·1	34·0 ± 9·9	58·4 ± 16·4
South African fruits 1980	1·4 ± 3·0	2·3 ± 4·0	96·3 ± 6·3	1·2 ± 2·8	19·9 ± 13·8	77·0 ± 17·2
South African fruits 1981	2·2 ± 1·8	10·2 ± 13·2	89·6 ± 12·5	11·8 ± 9·9	26·2 ± 17·5	63·4 ± 18·7

DISCUSSION

The low success obtained in the 1980 release is attributable to the high percentage (34.1%) of fruits infested using the least successful drilling position 4, and the lower efficiency of workers 2 and 3 (who together released 80.9% of the fruits).

Inspection of the naturally infested Australian fruits revealed that very few of the successful larvae had entered the seed cavity by a route corresponding with that of position 4; most had entered the fruits by a route corresponding to drilling position 2, the shortest route from the suture to the seeds. For this reason, and because of the relative lack of success obtained using drilling position 4 in the 1980 release, position 4 was not used for the 1981 release. Drilling position 1 was also excluded for the 1981 release because of the marked tendency of the larvae to enter the seeds in the posterior zone of the seed cavity.

Two points emerge from the comparison of the survival of the larvae of the 1980 and 1981 releases : there was a higher percentage of mortality in the early stages (1 and 2) in 1980 than in 1981, and a higher percentage of mortality at the later stages (5 and 6) in 1981 than in 1980. Mortality at the early stages is probably caused by workers whereas mortality at the later stages is more likely to be natural since these larvae died some time after they began to feed. In 1981, percentage mortality due to natural causes was higher than in 1980 because mortality due to artificial causes (handling) was lower.

The low number and percentage of larvae that died at stage 7 in 1981 compared with 1980 is due to the fact that most larvae dying at this stage in 1980 were placed in holes of drilling position 4, a method that was excluded in 1981. When using position 4, in which the drilled hole does not enter the seed cavity, it is easier to drill the hole in such a way that the distal end of the hole is off the suture. Observations show that the larvae practically always begin burrowing at the distal end of a drilled hole, and that if the end of the drilled hole is not on the suture, the larvae are unable to burrow through the woody fruit to the seed cavity, and die.

This study indicates that artificial methods of establishing insects in the field should correspond as closely as possible to the natural means of infestation to be most effective.

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Difficulties with the release and establishment of *Carposina autologa* Meyrick (Carposinidae) on the weed *Hakea sericea* (Proteaceae) in South Africa

by

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The moth *Carposina autologa* Meyrick was introduced from Australia to South Africa to reduce accumulated seed on the weed *Hakea sericea* Schrader. The previously devised methods of releasing the moth are reviewed, its level of establishment monitored at two sites, and reasons are given for the suspension of this programme in 1983.

INTRODUCTION

The woody shrub, ***Hakea sericea*** Schrader, is indigenous to south-eastern Australia. It was introduced to the south-western Cape Province of South Africa in the early nineteenth century and has subsequently become a major threat to the natural vegetation in nearly all the coastal mountain ranges of the Cape Province (Neser & Fugler 1978). At present, an estimated 480 000 hectares are infested in various degrees (Kluge 1983). Reasons for the invasiveness of this plant have been elucidated by Neser & Fugler (1978) and Neser & Annecke (1973).

Initial investigations on ***Carposina autologa*** Meyrick began circa 1965 and the programme was suspended in 1983. While this study was in progress, another seed attacking insect, the curculionid ***Erytenna consputa*** Pascoe, which attacks immature ***H. sericea*** fruits, was successfully established in South Africa as a biological control agent (Kluge & Siebert 1985; Neser & Kluge in press). The fungus ***Colletotrichum gloeosporioides*** (Penz.) Sacc. also became an important control agent which causes die-back and death of ***H. sericea*** (Morris 1982).

An important reason for the invasiveness of ***H. sericea*** in the Cape fynbos (macchia) is its copious production and accumulation of seeds which are released from the woody fruit (follicles) after fires (Neser 1968). Biological control using agents which reduce seed production seemed appropriate, hence the introduction of ***C. autologa*** to attack mature seeds in fruits which escaped ***E. consputa*** damage (Neser 1968). This paper records the releasing techniques used to establish C. ***autologa*** in South Africa, evaluative work done at a few sites where the moth was released, and the factors which resulted in the suspension of this project.

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BIOLOGY OF *C. AUTOLOGA*

C. autologa is univoltine with no diapausing or quiescent phases. The eggs which are laid in autumn hatch a few weeks later in winter. Larval development in the *H. sericea* fruits is completed in mid-summer, followed by pupation in the soil and emergence of the adults in autumn. The biology and host specificity of the moth have been studied in detail by Neser (1968).

The mature *H. sericea fruit* consists of two woody halves which enclose a cavity containing two winged seeds. There is a suture on the adaxial surface between the two halves of the fruit. This suture extends from the surface to the seed cavity. *C. autologa* moths lay eggs singly in protected sites on the rough fruit surface or between touching fruits. The newly-hatched larva penetrates the fruit along the suture and feeds on the seeds. During the third instar, the larva begins to prepare the exit tunnel, and after a process of alternating feeding and tunnelling, the mature larva leaves the fruit to pupate in the soil. The moths are crepuscular, feeding on flower nectar. Females may lay > too eggs.

MATERIAL **and METHODS**

Rearing and releasing techniques

Attempts were made to rear larvae on seeds and on artificial medium in the laboratory because of the losses that occurred when the larvae were reared individually on fruits on plants in walk-in cages or in the field. Rearing larvae on seeds was very labour intensive since the seeds had to be replaced because they germinated or became mouldy. The nutrient medium was based on. the meridic diet developed by Harley & Wilson (1968) to which ground *H. sericea* seeds were added. Adult production was low and unsynchronised, the length of the life cycle varied greatly, and many of the moths were deformed. Oviposition of caged adults was very unsatisfactory even though these moths were of normal size and had their abdomens distended with eggs.

In an attempt to overcome these negative effects, a drilling technique was developed whereby larvae were directly inserted into the *H. sericea* fruits in the field. Using a portable dental drill, a hole (approximately t mm in diameter) was drilled towards the seed cavity along the suture between the two halves of the fruits. A fine paint brush was then used to transfer larvae to the fruits and gently coax them into the drilled holes. The holes were sealed behind the larvae using a wax crayon, and the fruits were marked with coloured paint to facilitate their recovery for evaluation at a later stage. The larvae used were either newly hatched or had been feeding on medium fort to 4 weeks.

The advantages of this method were (a) better synchrony of the life cycle with the seasons (laboratory cultures produced moths all year round), (b) although initially time consuming, this method was less labour intensive than culturing moths throughout the year, and (c) larval survival would probably be higher because the larvae did not have to burrow into the fruits themselves, thus reducing the possibility of predation and other mortalities during penetration. Between 1978 and 1982, 515o larvae were inserted into fruits at six sites using this technique (Table r).

Despite the improvements of this rearing and releasing technique, problems were nevertheless encountered. Table **2** shows that only 48,4% of the eggs received from Australia in 1981 yielded larvae that could be successfully inserted into fruits, the

TABLE t. A chronological record of the number of *C. autologa* individuals released at six release sites. The majority (5150) of individuals released were larvae and the rest (4913) were released as moths at the first site in 1977.

Year	No. individuals released	Site	Co-ordinates
1977	498	Paradyskloof	18° 54′ S : 33° 58′ E
1978	217	Paradyskloof	18° 54′ S : 33° 58′ E
1978	541	Coetzenburg	18° 54′ S : 33° 56′ E
1979	455	Paradyskloof	18° 54′ S : 33° 58′ E
1980	1 065	Stellenbosch Mt.	18° 54′ S : 33° 57′ E
1981	574	Knorhoek	18° 57′ S : 34° 06′ E
1981	217	Stellenbosch Mt.	18° 54′ S : 33° 57′ E
1981	294	Paradyskloof	18° 54′ S : 33° 58′ E
1982	783	Wemmershoek	19° 08′ S : 33° 51′ E
1982	1 004	Goudini Spa	19° 16′ S : 33° 40′ E
Total	5 648		

heaviest mortality (38,1%) occurring in the egg phase. The drilling technique initially (1978-1979) yielded poor results because the drill bit used resulted in compaction of sawdust in the holes preventing larval penetration, or the drilling damaged the seeds making them susceptible to fungal attack. Another cause of larval mortality was the spray-paint used to mark the fruits. This was later found to be toxic to the larvae. With various modifications, this technique was improved considerably (Dennill 1987), and the rate of larvae successfully developing to the pupal phase increased from about 15% in 1979 to 65% in 1981.

Methods for the evaluation of C. *autologa* establishment

At Paradyskloof (near Stellenbosch) 498 moths were released in 1977, and from 1978-1981, g66 larvae were released using the drilling technique. At Stellenbosch Mountain, 1282 larvae were released using the drilling technique in 198o and 1981

TABLE 2. Mortalities of *C. autologa* eggs and larvae during the phases of rearing and releasing in 1982.

Phase	No. eggs/larvae	Percentage
Eggs imported 3692		
Eggs failing to hatch	1 407	38,1
Larvae died on medium	375	10,2
Larvae lost in medium	35	0,9
Larvae lost during releasing	61	1,7
Larvae killed accidentally during releasing	27	0,7
Total mortality	1 905	51,6
Total successfully inserted	1 787	48,4

TABLE 3. The vertical distribution of *H. sericea* fruits and fruits infested by *C. autologa* on six trees at Paradyskloof in 1981.

Height (m)	Total No. fruits	No. fruits infested	Proportion fruits infested*
0–1	519	55	0,106
1–2	1 360	43	0,032
2–3	2 090	32	0,015
3–4	2 287	14	0,006
4–5	243	0	0,000
Total	6 499	144	

•=This negative linear trend for the proportion of attacked fruits to vary with plant height is statistically significant (P=0.04) (Snedecor & Cochran, 1g67 pp.246-248).

(Table 1). At each of these release sites, a grid was laid out with the release point more or less central. The Paradyskloof grid was 5o m x too m and the Stellenbosch Mountain grid was too m x too m. Trees were marked at to m intervals in the grids. These trees were examined annually to determine whether there were any increases in infestation levels and to monitor moth dispersal. The abundance of fruit on hakea trees necessitated the design of a sampling technique for the taking of representative fruit samples.

The vertical distribution of the infested hakea fruits was used as a basis for sampling. Six trees at various distances from the release point were felled and the fruits in each vertical one-metre zone counted, noting the number which had *C. autologa* emergence holes. Only six trees were examined to minimise loss to the low moth population. The results (Table 3) showed that although only 7,3% of the fruits on the sampled trees occurred in the bottom metre, 38,2% of the attacked fruits were located in this zone.

To monitor *C. autologa* populations at Paradyskloof, the fruits in the bottom metre of the grid trees were sampled while at Stellenbosch Mountain the fruits in the bottom one-and-a-half metres were sampled. At the latter site the dense undergrowth

TABLE 4. *C. autologa* infestation levels on *H. sericea* trees in grids at two sites in the south-western Cape, and the number of trees killed by the fungus *C. gloeosporioides* from 1982 to 1984.

Year	No. fruits sampled	No. (&%) fruits with emergence holes	No. trees sampled	% trees diseased
A. PARADYSKLOOF SITE				
1982	1 406	73 (5.2)	41	7,0
1983	550	31 (5.6)	31	44,0
1984	162	0 (0,0)	9	88,4
B. STELLENBOSCH MOUNTAIN SITE				
1982	1 774	3 (0,2)	65	0,0
1983	1 605	1 (0,1)	57	12,3
1984	1 206	1 (0,1)	36	32,3

caused few fruits to be borne in the bottom half meter of the trees. The attacked fruits were counted annually from 1982 to 1984. Grid trees that were dying or dead because of attack by the fungal pathogen *C. gloeosporioides* were also noted.

RESULTS

Although fresh emergence holes confirmed that C. *autologa* was present at both sites throughout the study period, infestation levels were generally low and decreased during the sampling period (Table 4). The decrease in the number of fruits sampled over the study period at both sites was due to the increasing number of trees killed by *C. gloeosporioides* (Table 4), resulting in the suspension of further evaluation at these sites.

DISCUSSION

C. autologa has established at at least six sites in South Africa, but as yet no increases in the populations have occurred. This could be the result of adverse climatic or biotic factors, or factors responsible for numbers being below a critical level necessary for colonisation such as: (I) too few larvae were initially released; (2) the difficulty of mate-finding at low population levels; (3) the insect's univoltinism and (4) predation by generalised predators such as mites. The insect originates from high and constant rainfall regions in Australia and the occasionally dry autumns in South Africa may be unsuitable to some developmental stages. The difficulty of isolating biotic interference from other factors preventing establishment or colonisation of biological control agents has been reviewed by Goeden & Louda (1976).

Apart from the uncertainty of achieving successful establishment using the labour intensive techniques reviewed above, a number of other factors also contributed to the decline in the importance of *C. autologa as* a control agent against *H. sericea.* These were the increasing effectiveness of mechanical control measures (Fenn 1979); the efficiency of another control agent *E. consputa* (Kluge & Siebert 1985); the destructiveness of the fungus *C. gloeosporioides* (Kluge & Richardson 1983), which kills trees and subsequently all stages of *C. autologa* present; and the increasing importance of other weeds *e.g. Acacia longfolia* (Andr.) Willd. which invaded areas successfully mechanically cleared of *H. sericea.*

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