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Biological control of *Sesbania punicea* (Fabaceae) in South Africa

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ABSTRACT

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Sesbania punicea (Cav.) Benth., a South American leguminous shrub or small tree, has recently become a weed, principally of river banks and of wetlands, throughout South Africa. Three weevil species have been introduced for its biological control: a florivorous apionid, *Trichapion lativentre* (Bèguin-Billecocq), that was inadvertently introduced in the 1970s, and two curculionids that were first released in 1984, a seed-feeder, *Rhyssomatus marginatus* Fahraeus, and a stem borer, *Neodiplogrammus quadrivittatus* (Olivier). The reproductive potential of *S. punicea* has been markedly reduced throughout South Africa by *T. lativentre* and, to a lesser extent, by *R. marginatus*. In the vicinity of release sites, many large *S. punicea* plants have been killed by *N. quadrivittatus* and the density of at least one infestation has been reduced to acceptable levels within 4 years. A critical assessment of this biocontrol programme is presented.

INTRODUCTION

Sesbania punicea (Cav.) Benth. (Fig. 1) is a leguminous shrub or small tree that has pinnate compound leaves, showy inflorescences of bright red and orange flowers, and characteristic longitudinally winged pods. Its native range in South America extends from eastern Argentina, through Uruguay into southeastern Brazil (Erb, 1980). The attractiveness of *S. punicea*, especially when in flower, makes it a desirable ornamental species (e.g. Betto, 1977) and consequently it has been translocated between continents and has become a weed in both South Africa (Pienaar, 1978) and the southeastern USA (Holm et al., 1979).

In South Africa, *S. punicea* is mainly a problem along river banks and in wetland areas where it forms dense impenetrable thickets that exclude native plants and restrict access to water bodies and rivers (Hoffmann and Moran, 1988). The formation of dense thickets in river beds also hampers water flow, particularly during flooding, so that the rivers and streams burst their banks,

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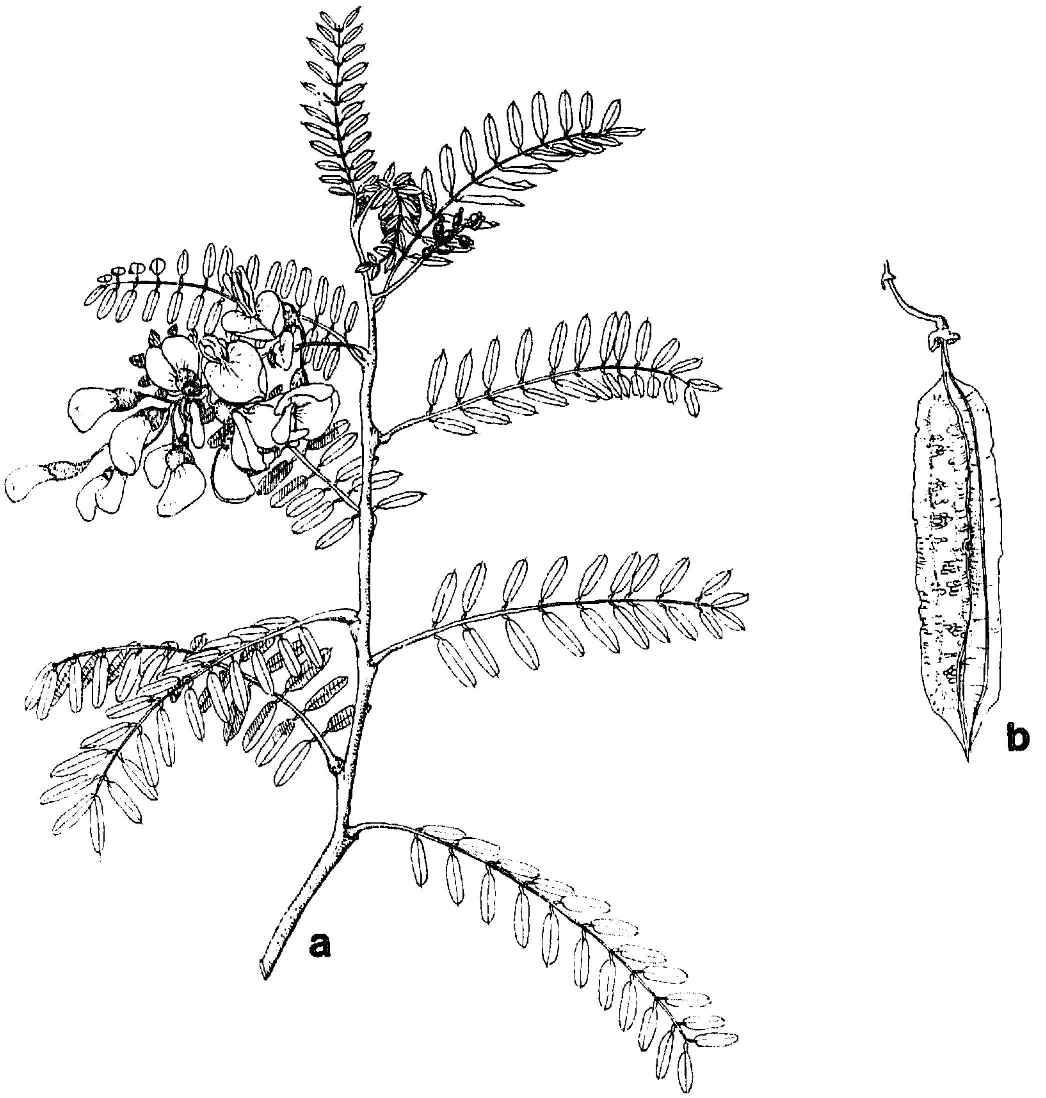

Fig. 1. *Sesbania punicea*. (a) Shoot with flowers; (b) mature pod. (Drawn by R. Weber, National Botanical Institute, Pretoria.)

causing lateral erosion of the water course (Hoffmann and Moran, 1988). In addition, all parts of the plant, but especially the seeds, are toxic (Duncan et al., 1955; Terblanche et al., 1966). However, reports of poisoning of livestock are apparently rare and seldom verified.

The biological control campaign against *S. punicea* in South Africa is notable for the short interval between the recognition of the plant's invasive abilities (Terblanche et al., 1966) and the initiation of the biocontrol programme. In an attempt to 'nip the problem in the bud', surveys for potential control agents commenced in 1972, 7 years before *S. punicea* was officially proclaimed a weed.

In spite of this timely commencement, the biological control programme against *S. punicea* faltered during its early stages, regained some momentum during 1980, before really getting underway in 1982 when four weevil species were introduced into quarantine in South Africa. By the end of 1984, one of the weevils was found to be well established on *S. punicea*, through a much earlier inadvertent introduction, and two of the other three species had also been released and had established on the weed (Hoffmann and Moran, 1988).

This review summarizes the biological control campaign against *S. punicea* in South Africa, highlighting problems that were encountered and discussing how they might have been avoided to improve the efficiency of the programme.

INTRODUCTION AND SPREAD OF *S. PUNICEA* IN SOUTH AFRICA

The earliest record of *S. punicea* in South Africa is from 1858 when the species was included under one of its synonyms, *Daubentonia punicea*, in a list of plants growing in the Cape Town Botanic Gardens (McGibbon, 1858). Other early records come from two herbarium specimens collected in the Transvaal during 1914 and 1916 (Hoffmann and Moran, 1988).

In spite of its prolonged presence in South Africa, *S. punicea* was apparently not a problem before the 1960s because it was not mentioned by Henderson and Anderson (1966) in their comprehensive list of weeds in South Africa. Neither was it included in two other floral lists compiled during the 1960s which incorporated alien plant species (Martin and Noel, 1960; Smith, 1966). However, the invasive potential of *S. punicea* was recognized at about this time by Terblanche et al. (1966) and, from 1974 onwards, *S. punicea* was reported as a weed in several published articles (e.g. Taylor, 1974; Anon., 1976; Haig, 1977; Pienaar, 1977, 1978).

Undoubtedly, domestic plantings throughout the country produced the seeds that 'escaped' and pioneered infestations of the weed. Consequently, *S. punicea* has invaded, to varying extents, many river systems throughout South Africa, but particularly in the moist eastern areas and in the Western Cape. In the winter-rainfall regions of the Western Cape Province, *S. punicea* only survives in the proximity of perennial water bodies where there is sufficient moisture for seedlings to survive during the dry summers. In the summer-rainfall regions (Natal and Transvaal), *S. punicea* is less dependent on perennial water sources and the plant has also become a weed in agricultural, range and forested lands (Duggan and Henderson, 1982; Henderson and Musil, 1983; Macdonald and Jarman, 1985; Macdonald et al., 1985; Geldenhuys et al., 1986; Henderson and Wells, 1986). There is little doubt that *S. punicea* has far from realized its full invasive potential and many riverine habitats, in particular, remain threatened by this plant.

BIOLOGICAL CONTROL

In 1972, the search for potential biocontrol agents of *S. punicea* commenced on both *S. punicea* and the closely related species *Sesbania virgata* (Cav.) Pers. (H.G. Zimmermann, personal communication, 1990). Eighteen species of insect herbivores with biological control potential were identified (Erb, 1980). Among these, two seed-feeding weevils, *Rhyssomatus marginatus* Fahraeus and *Apion decipiens* Bèguin-Billecocq, were considered to be the most suitable candidates for introduction into South Africa because, besides their apparent host specificity, they destroyed up to 90% of the seeds set by *S. punicea* and *S. virgata* in Argentina (Erb, 1980). It was hoped that similar, or greater, levels of seed destruction by the weevils, if successfully established in South Africa, would check the spread of *S. punicea* before it became a major weed problem.

No further progress was made for about 7 years because of staff shortages and the low priority afforded *S. punicea* as a weed. However, during January 1980, the first of nine consignments, each of which contained one or more of five weevil species, was air freighted to South Africa (Table 1). The five species included the two seed-feeding weevils, *R. marginatus* and *A. decipiens*, a bud-feeding apionid, *Trichapion lativentre* (Bèguin-Billecocq), a stem-boring curculionid, *Neodiplogrammus quadrivittatus* (Olivier) and a root-feeding curculionid, *Eudiagogus episcopalis* (Schoenherr).

Eight months after its initial introduction, during September 1982, the insectary colony of *E. episcopalis* was deliberately destroyed, as were all subsequent consignments of this weevil, because their larval damage to roots of potted *S. punicea* plants was negligible and because the insects proved difficult to handle in quarantine (Hoffmann and Moran, 1988). However, *E. episcopalis* is probably host specific because the genus *Eudiagogus* is almost exclusively associated with species of *Sesbania* and because *E. episcopalis* has only been recorded from *S. punicea* itself (Warner, 1979). Specificity tests are currently being conducted on *E. episcopalis* in Argentina, South America (H.G. Zimmermann, personal communication, 1990), with a view to its possible introduction into South Africa in the future. *Eudiagogus episcopalis* is not considered further in this review.

Apion decipiens was represented in small numbers in the shipments with only seven adults from *S. virgata* included in one consignment. These adults never produced any progeny and *A. decipiens* also receives no further consideration here.

The other three species are currently playing important roles in the biological campaign against *S. punicea* in South Africa and their case histories follow.

TABLE 1

Chronological record of the consignments of insect herbivores sent to South Africa for biological control of *S. punicea*. The approximate (in parentheses) or actual numbers consigned are recorded where known

Date	Origin	Collector	Host species	Agent	Number consigned
30/1/80	Tucuman, Argentina	H.E. Erb	*S. virgata*	*R.m.*	(300)
25/3/81	Tucuman	H.E. Erb	*S. virgata*	*R.m.*	?
17/2/82	Tucuman	H.E. Erb	*S. virgata*	*R.m.*	1817
				T.l	8
				A.d	7
5/9/82	Zarate, Argentina	H.G. Zimmermann and L. Mendoza	*S. punicea*	*T.l*	(200)
				E.e	(20)
?/12/82	Zarate	L. Mendoza	*S. punicea*	*R.m.*	?
				T.l	?
				E.e	?
				N.q	2
?/12/83, ?/1/84 and 6/2/84	Zarate	L. Mendoza	*S. punicea*	*R.m.*	?
				T.l	?
				E.e	?
20/9/84	Zarate	S. Neser and V.C. Moran	*S. punicea*	*N.q*	37
?/4/87	Port Alegre Brazil	S. Neser	*S. marginata*	*N.q*	50

R.m. is an abbreviation for *Rhyssomatus marginatus*, *T.l* for *Trichapion lativentre*, *A.d* for *Apion decipiens*, *E.e* for *Eudiagogus episcopalis* and *N.q* for *Neodiplogrammus quadrivittatus*.

TRICHAPION LATIVENTRE

Following initial surveys, Erb (1980) ranked *T. lativentre* low on the list of potential biocontrol agents for *S. punicea* because in South America the adults, although present on *S. punicea* and *S. virgata* throughout the year, were always relatively scarce and the biology of the immature stages of *T. lativentre* was unknown.

Biology of T. lativentre

The adults of *T. lativentre* are small (2–3 mm in length), mostly black, but with a patchy covering of white pubescence. The apparent blue colour of the elytra described by Bèguin-Billecocq (1909) is really a faint blue iridescence and only noticeable under certain light conditions. The adults fly readily and disperse over large distances, mostly in late summer and autumn when there are no flower buds on the plants which have started senescing for winter (Moran and Hoffmann, 1989).

The adults feed on the new leaflets, creating a characteristic shot-hole effect, and on the small flower buds, which then abort prematurely. After mating, the females oviposit in the tips of flower buds that have reached approximately 4 mm in length, when the petals have protruded beyond the calyx. The eggs, usually one per bud, are placed among the anthers and hatch within 2 days.

The larvae feed on the immature anthers and carpels within the bud. They develop rapidly on this nutrient-rich food source and reach maturity in about 4–5 days. Pupation occurs in the hollowed-out bud and lasts about 3 days, giving a total generation time from oviposition to adult eclosion of only 10 days in mid-summer (Hoffmann and Moran, 1988). As a result, there are several generations per annum and, when buds are present on the plants, populations of the weevils increase to densities that average up to 75 adults per 30 cm of stem. During winter, there is a steady decline in the populations of the weevils from mortality and dispersal losses (Hoffmann, 1988; Moran and Hoffmann, 1989).

Introduction of T. lativentre *into South Africa*

The introduction of *T. lativentre* into South Africa was notable for the fact that a thriving colony of the weevils was already established in quarantine insectaries at Rhodes University, Grahamstown, and host-specificity tests had commenced there when, on 13 October 1983, a population of *T. lativentre* was found on *S. punicea* plants along the Steincoalspruit river near Wasbank (28°21'S 29°58'E) in Natal. Subsequently, *T. lativentre* was found to be widespread throughout Natal and extended along the coastal belt as far south as East London (33°00'S 27°54'E).

It was then revealed that *T. lativentre* had been collected on 26 January 1981 alongside the N3 freeway close to the airport (29°56'S 31°00'E) at Durban, Natal (M.J. Morris, personal communication, 1984). A batch of these adults was caged for a short period on harvested branches of *S. punicea* and, although eggs were laid in the growing tips of the branches no progeny were obtained, presumably because there were no flower buds present. In addition, adults of *T. lativentre* were collected on 27 October 1982 from *S. punicea* growing on the banks of the Mkozi river near Amanzimtoti (30°03'S 30°53'E), Natal (C.J. Cilliers, personal communication, 1984). Unfortunately, the significance of these discoveries was not realized at the time and, although specimens (accession number AcPl 2112) were deposited in the National Collection of Insects, Pretoria, they were not then identified as *T. lativentre* and no further reports were made.

Speculating on the circumstances surrounding the arrival of *T. lativentre* in South Africa, Hoffmann and Moran (1988) stated that "*T. lativentre* was inadvertently introduced... probably by tourists from South America".

Therefore, it may be no coincidence that the weevils were first found in the proximity of the airport at Durban, which was frequented by Argentinean tourists during the late 1970s. However, the exact date, mode of translocation and number of *T. lativentre* introduced will never be known, although it seems most likely that there was a very small founder colony, possibly even a single gravid female.

Soon after the existence of viable populations of *T. lativentre* in South Africa was confirmed, the quarantine insectary colony in Grahamstown was destroyed. The disclosure that a potential biocontrol agent of *S. punicea* was readily available within South Africa resulted in a rush by entomologists, extension officers, land owners, municipal and conservation authorities, and other interested parties to collect and redistribute the weevils throughout the country. This, together with rapid natural dispersal of the insects, meant that within 3 years populations of *T. lativentre* were established on *S. punicea* throughout South Africa (Hoffmann and Moran, 1988).

Impact of T. lativentre *on* S. punicea

Soon after its discovery in South Africa, sampling programmes were conducted to assess the impact that *T. lativentre* was having on the reproduction and vegetative growth of *S. punicea* (Harris and Hoffmann, 1985; Hoffmann, 1988). Surveys showed that *T. lativentre* usually reduced pod production by more than 98% in moderate to dense infestations of the weed (Hoffmann and Moran, 1989; Moran and Hoffmann, 1989; Hoffmann et al., 1990). However, the weevils were less damaging on isolated plants and overwintering survival of adults was variable. Low winter survival intermittently retards the effectiveness of *T. lativentre* in some areas.

Although the impact that *T. lativentre* had on the growth, phenology and fecundity of *S. punicea* was clearly demonstrated (Hoffmann et al., 1990), the fundamental question of how this damage affects the population dynamics, and thus the density, of the weed still needs to be resolved. In the case of agents, that reduce the reproductive capacity of the weed, such as *T. lativentre*, there may be a long delay between the introduction of the agent and eventual decline of the weed (Holloway, 1964; Cohen, 1968). The rate of decline depends largely on the extent and longevity of the 'seed bank' in the soil and the rate at which existing plants die or are otherwise removed from the population.

Sesbania punicea plants seldom live for more than 10 years (J.H. Hoffmann, unpublished results, 1990). The seeds germinate readily and probably do not form extensive seed banks in the soil (Graaff and van Staden, 1984). The interval between the introduction of *T. lativentre* and a noticeable decline in the weed infestations was predicted to be about 14 years, assuming that the weevils were successful (Hoffmann, 1990). In order to determine the probable effectiveness of *T. lativentre*, a simulation model was developed and used to identify short-term changes in the weed infestations that might be indicative of longer-term trends (Hoffmann, 1990).

The model showed that greater than 98% seed reduction decreased seedling recruitment sufficiently to provide satisfactory control of the weed and that, in the declining populations of the weed, seedlings and 1-year-old plants no longer dominated the age structure of the infestations (Hoffmann, 1990). Therefore, changes in the age structure of the plants in infestations of *S. punicea* could provide an early indication of whether *T. lativentre* will control the weed or not and may facilitate decisions about the need for additional agents.

Infestations of *S. punicea* throughout South Africa are currently being monitored to determine how their age structures have changed since *T. lativentre* was introduced. Preliminary results show that *T. lativentre* alone may bring the weed under control (J.H. Hoffmann, unpublished results, 1990). However, the weevils tend to aggregate in dense infestations of *S. punicea* and are less active on sparse or isolated plants. As a result, *T. lativentre* may become less effective as a biological control agent as the density of the infestations of *S. punicea* decline, suggesting that even better control will be achieved by the introduction of additional agents.

RHYSSOMATUS MARGINATUS

This curculionid weevil is also found on both *S. punicea* and *S. virgata* in Argentina (Erb, 1980), and was rated as the prime candidate for introduction into South Africa because of the high levels of seed damage inflicted by its larvae on *S. punicea* in South America (Erb, 1980).

Biology of R. marginatus

The biology of *R. marginatus* is described in detail by Bruch (1907). The adults range from 4 to 8 mm in length and are dark grey to black with a characteristic faint white margin around the prothorax and lateral margins of the elytra (from which the specific epithet is derived).

The females lay their eggs in the mature, but unripe pods of *S. punicea*, depositing them against the seeds, usually at the extremities of the pod. The larvae feed within the pod and each one usually requires two to three seeds to complete its development. On reaching maturity, the larvae chew their way out of the pods, drop to the ground and tunnel a few centimetres into the soil. The prepupae then construct a chamber of compacted soil in which they lie dormant for the winter. Pupation occurs in spring and lasts for 2–3 weeks. After eclosion, the adults dig their way to the soil surface and climb or fly to the tree canopy where they feed on leaves, flowers and small pods, mate and oviposit.

Introduction of R. marginatus *into South Africa*

Although it had been decided that *R. marginatus* should be collected from *S. punicea* at Zarate (34°07′S 59°00′W) in Argentina (H.G. Zimmermann, personal communication, 1990), the first three consignments of weevils originated from *S. virgata* near San Miguel de Tucuman (26°47′S 65°15′W), Argentina (Table 1). All attempts to initiate insectary colonies with this material ended in failure (Van den Berg, 1981; C.J. Cilliers, personal communication, 1986).

The rapid deterioration of seeds in harvested pods and/or the unsuitability of an artificial diet, compounded by caging and insectary effects, were presumed to have prompted the demise of the first consignments of *R. marginatus* from *S. virgata* (Van den Berg, 1981; C.J. Cilliers, personal communication, 1986). However, it is now considered much more likely that *S. virgata* and *S. punicea* in Argentina may host different subspecies of *R. marginatus*, or possibly even two different species of *Rhyssomatus*, and the weevils from *S. virgata* were inherently unable to survive on *S. punicea*.

This supposition is supported by the fact that no problems were encountered in initiating colonies with *R. marginatus* adults that were collected from *S. punicea* at Zarate, Argentina (Table 1). These females readily oviposited in pods on harvested branches of *S. punicea* and, unlike the progeny from the adults that were collected on *S. virgata*, most of the larvae survived, pupated normally and large numbers of viable adults were obtained.

Specificity tests were conducted on *R. marginatus* during the 1982/83 and the 1983/84 austral summers. During starvation and choice tests, the adults fed on *Sesbania bispinosa* (Jacq.) W.F. Wight. However, this did not preclude *R. marginatus* from consideration for release because no oviposition occurred, the negligible damage was confined to foliage (J.H. Hoffmann, report on file, Plant Protection Research Institute, Pretoria, 1984), and the indigenous status of *S. bispinosa* in South Africa is doubtful (Phillips and Hutchinson, 1921; Gillett, 1963; Gibbs Russell, 1984). The screening tests showed that *R. marginatus* was able to utilize only *S. punicea* as a host in South Africa and permission to release the weevil was granted on 27 April 1984.

Releases commenced the following summer and two populations of the weevil were successfully established at East London, where 133 adults were released on 31 October 1984, and at Burntkraal farm (33°15′S 26°32′E) near Grahamstown where 166 adults were released between 30 November 1984 and 14 January 1985. The insectary colony of *R. marginatus* was maintained until it was confirmed that *R. marginatus* had survived through the winter and adults could be collected in the field for redistribution. Table 2 summarizes the releases and redistribution of *R. marginatus* in South Africa. A complete diary is on file at the University of Cape Town (Hoffmann, 1990).

In one case, establishment of *R. marginatus* was achieved with only 27

TABLE 2

Summary of releases of *R. marginatus* adults in different regions of South Africa from 1984 to 1990. Both the number of adults and the number of batches released (in parentheses) are shown

Fruiting season	East Cape	Natal	West Cape	North Transvaal	Total
1984/85	382(4)*	35(1)*	-	-	417 (5)
1985/86	27(1)	55(1)*	60(1)	-	142 (3)
1986/87	100(2)	-	140(2)	-	240 (4)
1987/88	-	-	-	-	-
1988/89	90(2)	238(2)	160(4)	450(2)	938(10)
1989/90	100(1)	250(4)	64(1)	150(1)	564 (8)
Total	699(9)	578(4)	424(7)	600(2)	2301(22)

*Releases of insectary-reared adults.

adults, although usually between 50 and 100 adults were released at each site. The presence of larvae in a second or subsequent generation following release has been confirmed at 55% of the sites where releases were made before February 1987. No releases were made during the 1987/88 summer and it is too early to confirm establishment from releases made during the 1988/89 summer. All the sites where populations of *R. marginatus* failed to survive had either been cleared manually (five sites) or burnt (one site) subsequent to the release of the weevils.

Impact of R. marginatus *on* S. punicea

Surveys throughout South Africa at sites where *R. marginatus* has been established for 3 or more years show that, unlike *T. lativentre, R. marginatus* showed no preference for either clustered or isolated plants and, on average, it destroys about 84% of the seeds that are set (J.H. Hoffmann, unpublished results, 1990). This level of mortality, together with the reduced seed set attributable to *T. lativentre*, has lowered the fecundity of *S. punicea* in South Africa by about 99.7%. Although surveys are still being conducted, early indications are that the dispersal and invasive potential of *S. punicea* has been severely curtailed by the combined action of *T. lativentre* and *R. marginatus.*

NEODIPLOGRAMMUS QUADRIVITTATUS

This stem-boring weevil is the only species introduced into South Africa that primarily damages the vegetative rather than the reproductive growth of *S. punicea.* Its univoltine habit and apparently low fecundity (Bruch, 1907) cast doubts on its potential to become an effective biological control agent. This opinion was reinforced by the fact that *N. quadrivittatus* shares these potentially negative characteristics with the cactophagous weevil borer, *Metamasius spinolae* (Gyllenhal), which although established on *Opuntia ficus-indica* (L.) Miller locally, has not dispersed more than 1 km from the original release sites in the 37 years since its release. It has had a negligible impact on the weed (Pettey, 1953; Annecke and Moran, 1978).

Biology of N. quadrivittatus

Of the three weevil species introduced onto *S. punicea* in South Africa, the adults of *N. quadrivittatus* are the largest (8–10 mm, excluding the rostrum) and most colourful, with an apparently mimetic association with the smaller, but similarly coloured, root-feeding weevil *E. episcopalis*. The adults lived for up to 2 years in the insectary and mated and laid eggs throughout their lives.

The female uses her mouthparts to excavate a hole in a branch or stem of *S. punicea*. A single egg is deposited in the hole which is sealed with regurgitated plant tissue that dries to form a dark, cryptic, hard plug. The larvae feed beneath the bark, destroying the vascular tissues and effectively 'ring-barking' the plants. They tunnel downwards, often reaching the root crown at the base of the stem, where the plant is most susceptible to their feeding damage. As a result, large *S. punicea* trees may be killed by small numbers of larvae. The larvae develop slowly, requiring 9–10 months to complete their life cycle (Bruch, 1907).

Introduction of N. quadrivittatus *into South Africa*

The first consignment of *N. quadrivittatus* comprised only one pair of adults from *S. punicea* at Zarate (34°07′S 59°00′W). These were sleeve-caged on potted *S. punicea* plants into which the female laid eggs. The larvae developed in the plants and produced a generation of adults about 10 months later.

Specificity tests were successfully completed (J.H. Hoffmann, report on file, Plant Protection Research Institute, Pretoria, 1984) and permission to release *N. quadrivittatus* was granted on 27 April 1984. The results of the specificity tests showed that *N. quadrivittatus* would probably feed and oviposit on some indigenous *Sesbania* species in South Africa. However, this was not considered a problem because the native species are mostly fast growing, annual or biennial species (Phillips and Hutchinson, 1921) which would mature and set seeds before the univoltine weevil larvae could complete their development and cause much damage. Also, the threat that indigenous plant species face from invasions by *S. punicea* was considered to be much greater than that posed by the weevils. Since its introduction, *N. quadrivittatus* larvae have been collected in small numbers feeding in *Sesbania macrantha* Phill. and Hutch. along the Sand River near Hazyview (25°02′S 31°09′E) in the eastern Transvaal.

A second consignment of 37 adults, also from Zarate, was incorporated into

TABLE 3

Summary of releases of *N. quadrivittatus* in different regions of South Africa from 1984 to 1990. Both the number of adults and the number of batches released (in parentheses) are shown

Year	East Cape	Natal	West Cape	North Transvaal	East Transvaal	Total
1984	90(1)*	-	-	-	-	90 (1)
1985	124(2)*	32(1)*	-	-	-	156 (3)
1986	50(1)	-	81 (3)*	22(1)*	-	153 (4)
1987	145(2)	70(1)	369 (4)	200(1)	-	784 (8)
1988	-	-	564 (5)	223(4)	214(2)	1001(11)
1989	32(1)	-	207 (2)	-	104(2)	343 (5)
1990	-	264(1)	-	-	-	264 (1)
Total	441(6)	366(3)	1221(14)	445(6)	318(4)	2791(33)

*Releases of insectary-reared adults.

the original insectary colony on 7 September 1984. A third consignment of 50 adults from *S. marginata* near Porto Alegre (30°03'S 51°10'W), Brazil, was released directly onto *S. punicea* in an isolated infestation of the weed near Swartruggens (25°40'S 26°42'E) in the Western Transvaal to prevent it from mixing with the populations from Zarate, Argentina.

The first releases of *N. quadrivittatus* were made with insectary-reared adults at Burntkraal Farm near Grahamstown on 17 August 1984 (Table 3). Releases with insectary-reared adults continued at other sites until December 1986, when adults could be collected at the first release site in sufficient numbers for redistribution.

Establishment of *N. quadrivittatus* has been confirmed at 9 of the 22 sites at which it was released before June 1988 (J.H. Hoffmann, unpublished results, 1990). The releases that have failed are attributed to clearing or burning of the host plant (six sites) and to releases made at the wrong time of the year, in autumn (seven sites). The adults lay few, if any, eggs during winter and natural dispersal may dilute the populations to the extent that problems are encountered with mate location.

Impact of N. quadrivittatus *on* S. punicea

Ongoing surveys are being conducted to quantify the impact that *N. quadrivittatus* has had since its release in South Africa, but the results are too preliminary to report here. However, at the first release site near Grahamstown, almost all of the mature plants have been destroyed by the weevils and the infestation of *S. punicea* has been reduced from a dense thicket to a few scattered saplings. Similar patterns of spectacular destruction are being witnessed at other, more recent, release sites and the prospects are extremely promising for dramatic biological control of *S. punicea* with *N. quadrivittatus*.

DISCUSSION

In terms of precedents in, and the theory of, biological control in general, the introductions of *T. lativentre, R. marginatus* and *N. quadrivittatus* onto *S. punicea* have some interest.

(i) The small founder colonies, particularly of *T. lativentre*, (possibly a single gravid female) and *N. quadrivittatus* (39 individuals), that pioneered the thriving populations now common in South Africa show that genetic bottlenecks (e.g. Remington, 1968; Myers and Sabath, 1981) need not necessarily be a problem with introductions of weevils for biological control. (ii) The three weevil species, originally collected in one small area of Argentina, became established throughout South Africa in a wide range of climatic zones, showing that ecoclimatic matching (e.g. Wapshere, 1981) need not be an important consideration in selecting biological control agents. (iii) The three successfully established species all originated from *S. punicea*, while none of the founder colonies from *S. virgata* survived when 'newly associated' (Hokkanen and Pimentel, 1984) with *S. punicea* in the insectary in South Africa. (iv) Predicting the effectiveness of biological weed control agents is hazardous; neither *T. lativentre* nor *N. quadrivittatus* was considered to be potentially useful and yet both species are having a substantial impact on the weed.

Considering the biological control programme against *S. punicea* more specifically, most problems arose because, in its initial stages at least, no one was directly responsible for the programme against *S. punicea* and the project was not formally registered until colonies of insect agents had been established in quarantine in South Africa. As a result, routine procedures were neglected with the following detrimental consequences.

There was a delay of some 8 years between the initiation of surveys for suitable biological control agents, during 1972, and the first introductions of agents into quarantine in South Africa during 1980. This delay, compounded by an initial failure to establish insectary colonies, allowed *S. punicea* a period of grace during which the weed expanded its range unhindered.

The shipments of *R. marginatus* from *S. virgata* were unsuccessful, probably because *S. punicea* was an incompatible host plant. Both time and money may have been saved by collecting the insects from *S. punicea* in the first place, as had been advocated.

An inadequate knowledge of the biology and phenology of *R. marginatus* caused problems on at least two occasions. Firstly, a shipment of *R. marginatus* was introduced too late in the summer and the weevils that arrived in South Africa failed to oviposit, either because they were senile or because no suitable pods were available. Secondly, a consignment of larvae of *R. margin-*

atus that remained in the pods for some months in the insectary was presumed to be inviable and was destroyed. Although this behaviour is not the norm (most larvae overwinter in the soil), it is certainly not unusual and had the larvae been maintained into summer, adults may have been obtained.

Timely surveys on *S. punicea* in South Africa would have exposed the presence of *T. lativentre* before the introduction of any of the agents. Efforts could then have been diverted to evaluate the impact that *T. lativentre* was having on *S. punicea* in this country. If *T. lativentre* had proved successful on its own, *R. marginatus* and *N. quadrivittatus* need not have been imported, with concomitant savings and avoidance of the risks that are associated with the release of every biological weed control agent.

Although not directly important from a biological control point of view, the rapid and haphazard distribution of the introduced insects, mainly by enthusiastic lay people, thwarted some aspects of the evaluation studies on the agents. The performance of agents acting alone and in different combinations could not be monitored because the authors were unable to prevent, or were not informed about, releases in or close to areas set aside for evaluation studies. In addition, the widespread releases meant that estimates of rates of dispersal were rendered unreliable. This type of problem was impossible to avoid once the availability of successful agents was publicized. Perhaps, future weed control programmes should be given less publicity and releases should be more strictly controlled, at least until evaluation studies are complete, or are at a stage where unplanned redistribution of the agents becomes irrelevant.

In biological weed control, it is widely accepted that more agents will achieve better control (Harris, 1981, 1984) and the temptation is to release agents as soon as they become available. It may be argued that unnecessary risks were taken with the biocontrol campaign against *S. punicea* because too many agents were released in too short a time and it now seems that any one of the three weevil species may have provided adequate control of the weed. Ideally, agents should be introduced one at a time, with successive introductions only being made once the agent has been thoroughly evaluated and the reasons for its inadequacy have been determined. Agents that suppress reproduction of the weed will usually require more evaluation time because they take longer to impact on the weed than those that destroy the standing plants. Unfortunately, land owners and funding agencies require that control of the weed be achieved as rapidly as possible and evaluation studies are considered a luxury.

On a positive note, the biological control programme against *S. punicea* has been undertaken, and a great deal has been achieved, at relatively litle expense. Both the original surveys for potential agents, and all subsequent collections, in South America were undertaken by biologists primarily involved in other biological control programmes, mainly against cacti, or by commissioned South American biologists. The programme is also notable for being an attempt to tackle the *S. punicea* problem at an early stage, before the weed infestations became too widespread, dense and otherwise unmanageable.

The results achieved so far have exceeded expectations and *S. punicea* must now be considered to be well on the way to being brought under effective biological control in South Africa.

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