A review of the agents and factors that have contributed to the successful biological control of *Sesbania punicea* (Cav.) Benth. (Papilionaceae) in South Africa

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An invasive, South American, perennial, leguminous tree, *Sesbania punicea* (Cav.) Benth., has been brought under biological control in South Africa as a result of the actions of three species of herbivorous insects, a bud-destroying apionid, *Trichapion lativentre* (Bèguin-Billecocq), a seed-feeding weevil, *Rhyssomatus marginatus* Fåhraeus, and a stem-boring weevil, *Neodiplogrammus quadrivittatus* (Olivier). Each of the three species has become abundant and damaging on the weed and together they cause sufficient damage to maintain their host plant at population levels that are no longer problematic. In this review, the results of several studies that have quantified the impact of the agents on the growth, reproduction and survival of *S. punicea* and on the population dynamics of the weed are summarized.

Key words: *Sesbania punicea,* biological weed control, growth, reproduction, survival, plant population dynamics.

Sesbania punicea (Cav.) Benth. (Fig. 1) is a perennial leguminous tree from South America that has invaded many parts of South Africa (Fig. 2), in particular rivers and water-courses where it restricts access, increases erosion and, through transpiration, depletes valuable water resources (Hoffmann & Moran 1988). In the 1980s a biological control programme was launched against *S. punicea* in South Africa and three species of weevils were released on the weed. These include *Trichapion lativentre* (Bèguin-Billecocq), whose larvae develop in and destroy the flower buds, *Rhyssomatus marginatus* Fåhraeus, whose larvae destroy the ripening seeds, and *Neodiplogrammus quadrivittatus* (Olivier), whose larvae develop in the stems and branches and thus kill the plants (Hoffmann & Moran 1988; Hoffmann 1990).

The biological control programme against *S. punicea* in South Africa was reviewed in 1991 in an article that described the introduction and spread of *S. punicea* in South Africa as well as the biology and releases of the three species of biological control agents that have been used against the weed (Hoffmann & Moran 1991a). At the time, there were few quantified observations of the impact of the agents on the weed and, more importantly, 'the fundamental question of how this damage affects the population dynamics, and thus the density, of the weed still need to be resolved' (Hoffmann & Moran 1991a).

Since 1991, several studies have enhanced our knowledge of the impact of the agents on the weed, including detailed long-term observations on changes in the population dynamics and density of *S. punicea* in South Africa (Hoffmann & Moran 1991b, 1992a,b, 1995, 1998; Strathie & Hoffmann 1993). As a result, we now have rigorous data that demonstrate that *S. punicea* is under excellent biological control in South Africa. The purpose of the present review is to summarize the most recent findings in support of this conclusion.

IMPACT OF THE AGENTS ON THE GROWTH AND REPRODUCTION OF *S. PUNICEA*

Trichapion lativentre

Under most circumstances, the bud-feeding weevil *T. lativentre* destroys almost all the buds on *S. punicea* in South Africa and, as a result, pod production by the plants is routinely reduced by more than 98 % (Hoffmann 1988; Hoffmann & Moran 1989; Moran & Hoffmann 1989; Hoffmann *et al.* 1990). However, there are at least two situations in which *T. lativentre* does not realize its full potential as a biocontrol agent.

Firstly, comparisons showed that *T. lativentre* was usually much more abundant on *S. punicea* plants growing in dense aggregations than it was on plants growing in relative isolation from conspe-

Fig. 1
***Sesbania punicea* shoot with flowers.**
(Drawn by W. Roux, National Botanical Institute, Pretoria.)

cifics (Hoffmann & Moran 1992a). A consequence of this is that a smaller proportion of flower buds are destroyed by *T. lativentre* on isolated plants and considerable quantities of seed continue to be produced by these plants in spite of the presence of *T. lativentre.* In the long term, this means that *T. lativentre* may become less effective as a biological control agent as thickets of the weed decline and the remaining plants become increasingly dispersed.

Secondly, *T. lativentre* has been found to be detrimentally affected by insecticidal drift from citrus orchards onto neighbouring infestations of *S. punicea.* In the Olifants River valley, Western Cape Province, which is a major citrus-producing area, the damage caused by *T. lativentre* has been sporadic and the *S. punicea* plants along some sections of the river continually produced large numbers of seeds (Hoffmann & Moran 1995).

Surveys along the Olifants River showed that the levels of pod production on *S. punicea* were affected by agricultural practices in the citrus orchards adjacent to infestations of the weed. Some of the citrus farmers relied on insecticides to control insect pests in their orchards whereas others depended predominantly on biological control and used insecticides sparingly. *Trichapion lativentre* was very abundant in infestations of

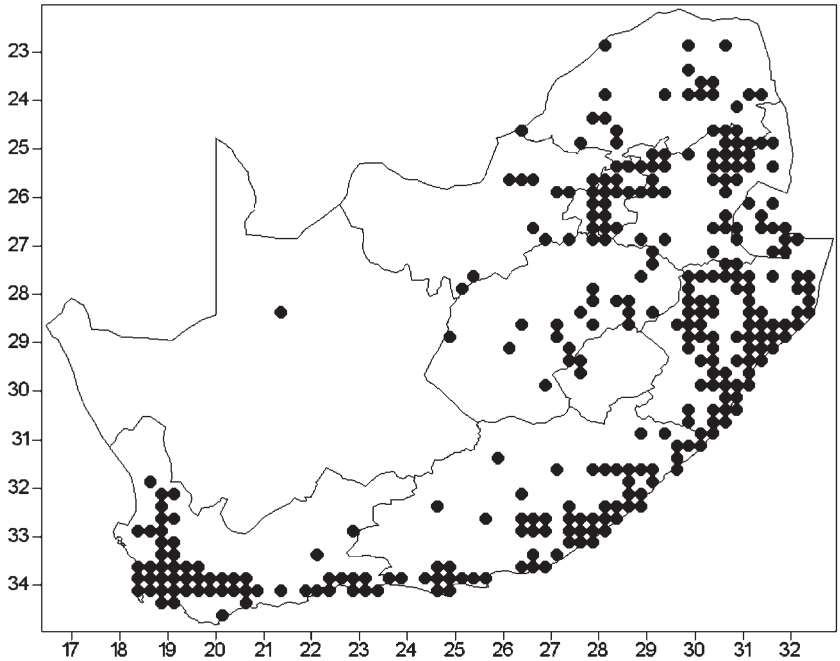

Fig. 2

Distribution of *Sesbania punicea* in South Africa.

(Drawn by L. Henderson, Plant Protection Research Institute, Pretoria.)

S. punicea bounded by citrus orchards under biological control and in areas without citrus orchards. In these situations the trees produced very few pods, whereas infestations along sections of the river bounded by citrus orchards under insecticide treatments produced large quantities of pods (Hoffmann & Moran 1995). The detrimental effect of the insecticides on *T. lativentre* was further demonstrated by the fact that in areas where *S. punicea* was growing in the proximity of citrus orchards under insecticidal control, levels of pod production increased significantly with distance to the nearest citrus plants (Hoffmann & Moran 1995).

In spite of these relatively minor and localized constraints, *T. lativentre* is an exceptional agent and has attained high population densities on the weed across a wide range of climatic conditions throughout South Africa. This widespread success is remarkable because *T. lativentre* became established in South Africa from 'a very small founder colony, possibly even a single gravid female' (Hoffmann & Moran 1991a). These observations are relevant in the context of the debates about the need for climatic matching of biological control agents (Wapshere 1985, 1993; Wapshere *et al.* 1989) and about minimal viable sizes of founder colonies (*e.g.* Remington 1968; Hopper *et al.* 1993).

Rhyssomatus marginatus

In spite of the extraordinary impact of *T. lativentre*, *S. punicea* still produces some seed pods and *R. marginatus* was introduced into South Africa to reduce seed production even further. The introduction has been a success because the larvae of *R. marginatus* destroy a considerable proportion of the seeds that are produced by *S. punicea* after *T. lativentre* attack.

The levels of seed destruction by *R. marginatus* were found to differ substantially at different localities. In the summer rainfall region almost 86 % of the *S. punicea* seeds were destroyed by *R. marginatus,* compared with only 49 % of the seeds in the winter rainfall regions over three seasons (Hoffmann & Moran 1992b). The causes for this difference are unknown. The overwintering survival of *R. marginatus* larvae and pupae under different conditions of soil type and moisture levels was investigated but found not to affect survival (Strathie & Hoffmann 1993).

An important contribution to the success of *R. marginatus* as a biological control agent is the meticulous oviposition behaviour of the females. The eggs are dispersed over the available food resources, which minimizes harmful intraspecific encounters between the developing larvae and, in the process, the number of seeds that are destroyed is maximized (Hoffmann & Moran 1992b). An important supplement to this behaviour is the fact that *R. marginatus* is equally damaging to seeds on isolated trees as on trees growing in dense thickets (Hoffmann and Moran 1992b). This implies that as *S. punicea* populations decline in density, and *T. lativentre* becomes less effective as a biological control agent, *R. marginatus* will become increasingly important.

Neodiplogrammus quadrivittatus

Hoffmann & Moran (1991a) described the impressive destructiveness of *N. quadrivittatus* at one site and this pattern has now been repeated at numerous sites across the country. As yet, no effort has been made to quantify the number of larvae that will kill a tree because the damage is so obvious, but this could be a fruitful line of research.

IMPACT OF THE AGENTS ON THE POPULATION DYNAMICS OF THE WEED

Although the studies outlined above provided important insights into the potential effectiveness of the introduced biological control agents, of critical importance is whether or not the damage caused by the agents is achieving the required degree of biological control (*i.e.* whether or not it can be demonstrated that the density or invasiveness of the weed has declined as a result of the agent attack). Two long-term studies have addressed these issues for the agents on *S. punicea* in South Africa.

Firstly, Hoffmann & Moran (1991b) showed that the density of *S. punicea* seedlings declined significantly in correspondence with the number of years that *T. lativentre* was present in the infestations of the weed. The decline was most rapid during the first five years following the establishment of *T. lativentre.* Generally the density of seedlings has remained at much lower levels since the release of *T. lativentre,* but this decline has not had a noticeable effect on the density of mature *S. punicea* plants in infestations of the weed. Apparently, *T. lativentre* has removed a massive excess of seeds that would have succumbed to self-thinning and other density-dependent factors during the early part of their growth (Hoffmann & Moran 1991b). Nevertheless, the reduction in seed production must have had a significant impact on the rate of dispersal of the weed into previously uninvaded regions and into areas where the weed has been controlled by non-biological methods (Hoffmann & Moran 1991b). This has created the impression that mechanical control of *S. punicea* is easy and successful since the introduction of *T. lativentre* because the weed does not readily repopulate cleared areas. Indeed, counts of *S. punicea* in at least one cleared area show this to be the case (unpubl. data).

Secondly, Hoffmann & Moran (1998) have shown that, in combination, the three species of agents released on *S. punicea* in South Africa are able to bring the weed under complete control. The weed was controlled in one of three infestations where *T. lativentre* and *R. marginatus* were present together and similarly, when *T. lativentre* and *N. quadrivittatus* were present together, control was achieved in two of six infestations. In the four instances that were monitored, where *T. lativentre, R. marginatus* and *N. quadrivittatus* were all present, the populations of the weed declined from more than 20 plants per 10 m^2 to less than one plant per 10 m^2 over a ten-year period and the weed was no longer considered a problem in these areas. The results of these long-term studies clearly showed that it was the combined action of the agents that had brought the weed under control and not the impact of any one of the agents.

CONCLUSION

Because considerably more effort has been spent on long-term evaluation studies of the biological control programme against *S. punicea* than is normally the case in biological control, it can now be stated unequivocally that *S. punicea* is under complete biological control in South Africa. It is almost a certainty that this result is because agents that neutralized the fecundity of the weed were used and this enabled the stem borer to realize its full potential as a biological control agent. This precedent supports the contention that 'agents that reduce seed set or destroy the seeds of their host plant should be used routinely as a first line of attack in the biological control of weeds' (Hoffmann & Moran 1998).

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