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The population dynamics of an introduced tree, *Sesbania punicea*, in South Africa, in response to long-term damage caused by different combinations of three species of biological control agents

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Abstract This paper contributes to the relatively sparse literature on the effects of insect herbivory on the population dynamics of plants and is probably unique in that it reports the long-term effects of combinations of three insect herbivore species on the population densities of a moderately long-lived tree species. The tree is *Sesbania punicea*, a leguminous perennial from South America that has been the target of a biological control programme in South Africa for almost 20 years. Sixteen infestations of the weed have been monitored for periods of up to 10 years to determine changes in the density of the mature, reproductive plants under the influence of different combinations of three biological control agents (i.e. with one, two or three of the agent species present in the weed infestation). The three biological control agents, all weevil species, include *Trichapion lativentre*, which primarily destroys the flower-buds, *Rhyssomatus marginatus*, which destroys the developing seeds, and *Neodiplogrammus quadrivittatus*, whose larvae bore into the trunk and stems of the plants. While *T. lativentre* occurs throughout the range of the weed in South Africa, the other two species are less mobile, more recent introductions and are largely confined to the vicinity of selected release sites. There has been a significant decline in the density of mature *S. punicea* in areas where two or more of the agents are established. The decline of the weed has been most evident where *N. quadrivittatus* is active and particularly so where both of the other two weevil species are also present.

Key words Insect herbivory · Host-plant density · Perennial weed · Biological control

Introduction

Almost all of the long-term observations on the effects of insect herbivores on plant population dynamics emanate from programmes on the biological control of weeds. Most of the studies have dealt with annual or biennial plants (e.g. Huffaker and Kennett 1959; Brown 1989; Myers et al. 1989; Kok and Mays 1991; McEvoy et al. 1991; Myers 1995; Coombs et al. 1996), but aquatic weeds (e.g. Thomas and Room 1986; Center et al. 1989; Grodowitz et al. 1991) and *Opuntia* species (e.g. Moran and Zimmermann 1991) have also received attention. There is no record that any attempt has been made to determine the effects of insect herbivory on the population dynamics of a perennial tree species. The study that is reported here deals with such a case.

The subject of this paper is the tree *Sesbania punicea* (Cav.) Benth. (Fabaceae) which is native to Argentina, Uruguay and Brazil and was introduced into South Africa at least 150 years ago (McGibbon 1858). The first reports of *S. punicea* being invasive in South Africa were made only in the 1960s, after which it spread rapidly and became an important weed in wetlands and rivers in the moister eastern parts of South Africa (Hoffmann and Moran 1988, 1991a). The trees grow to approximately 4 m in height and live for up to 15 years. They reach reproductive maturity after 2 years and produce an abundant crop of seeds each summer.

In its native South American range, *S. punicea* is utilised by at least 18 insect herbivore species that together conspicuously damage all parts of the plant (Erb 1980). In South Africa, *S. punicea* suffered negligible damage from a few local generalist insect herbivore species until the 1980s when three of the South American herbivore species, a bud-destroying and leaf-feeding apionid, *Trichapion lativentre* (Bèguin-Billecocq), a seed-feeding curculionid, *Rhyssomatus marginatus* Fahraeus, and a large stem-boring curculionid, *Neodiplogrammus quadrivittatus* (Olivier), were introduced into South Africa for biological control of the weed. The biology of the weevils,

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their population dynamics and their effects on the growth and reproduction of the weed have been reported elsewhere (Bruch 1907; Hoffmann 1988; Hoffmann and Moran 1989, 1992a, b; Hoffmann et al. 1990; Moran and Hoffmann 1989) and this biological control project has been reviewed by Hoffmann and Moran (1991a). In essence: (1) *T. lativentre* larvae develop within and destroy the flower-buds, and the adults feed on the leaves and flower-buds, causing a 98% reduction in the number of seeds produced and a 40% reduction in above-ground vegetative biomass; (2) *R. marginatus* larvae develop within, and destroy up to 90% of, the ripening seeds and the adults damage the leaves; and (3) *N. quadrivittatus* larvae develop in the woody stems, preferentially in the root-crowns, where the damage inflicted by only a few larvae can kill large mature trees, and the adults feed on the meristems and leaves.

We have shown that the 98% reduction in seed-set brought about by *T. lativentre* resulted in a highly significant and sustained reduction in the density of immature plants (pre-reproductive seedlings and 1-year-olds) 6 years and more after colonisation of the *S. punicea* patches by *T. lativentre* (Hoffmann and Moran 1991b). In spite of this dramatic decline in immature plants, the few seedlings that were produced were sufficient to replenish the mature plants in infestations of the weed and there was thus no corresponding decline in the density of mature plants as a result of the action of *T. lativentre* alone.

In this paper we report on the effects of the three weevil species, acting alone, in the case of *T. lativentre*, or as pairs of species or as all three species together, on the population densities of mature *S. punicea* plants (i.e. pod-producing trees ≥ 2 years old).

Materials and methods

Infestations of *S. punicea* were sampled at sites at 16 localities throughout South Africa. Originally 22 sample sites were estab-

lished but 6 of these were destroyed by fire or manual clearing operations during the course of the study and had to be discarded. The combinations of agents and the duration of their establishment at each site is given in Table 1. The sites were sampled five to eight times over a 10-year period between 1988 and 1997.

At each site on each sampling occasion, counts were made of the number of mature *S. punicea* plants within 2-m-wide transects. The number and length of the transects at each site depended on the extent of the infestation and on the density of plants, but most of the transects were 40 m long and there were usually three per site. Though not strictly permanent, the transects were laid as close as possible to the position of the corresponding transect from the previous sampling occasion.

The sample sites (Table 1) were categorised according to the combination of agents present, namely those with *T. lativentre* only (sites A–C), those with *T. lativentre* and *R. marginatus* (sites D–F), those with *T. lativentre* and *N. quadrivittatus* (sites G–L) and those with *T. lativentre*, *R. marginatus* and *N. quadrivittatus* (sites M–P). The rapid spread of *T. lativentre* into all of the survey sites made it impossible to observe the effects of *R. marginatus* and *N. quadrivittatus* on their own or in combination without *T. lativentre*.

The densities of plants were transformed (\log_{10} number $m^{-2} + 1$) and subject to linear regression analyses to show the trends of changes in density with time at each of the sites separately, as well as collectively for all of the densities that were measured within each of the four categories of agent combinations.

Results

The effects of the three weevil species, in different combinations, on the density of *S. punicea* trees over a 10-year period are shown diagrammatically in Fig. 1. The regression statistics for the scattergraphs are given in Table 2.

As had been noted previously (Hoffmann and Moran 1991b), the bud-feeding weevil, *T. lativentre*, alone, had no significant affect on the density of mature *S. punicea* plants (sites A–C). In areas where both *T. lativentre* and *R. marginatus* were present together, and seed-set of the plants was reduced by up to 99.7% (Hoffmann and Moran 1992b), there was a highly significant decline in the density of the mature *S. punicea* plants at one (site E)

Table 1 Locations of infestations of *Sesbania punicea* that were surveyed to determine the effectiveness of the three species of biological control agents, *Trichapion lativentre*, *Rhyssomatus marginatus* and *Neodiplogrammus quadrivittatus*, that had either immigrated into (years in parentheses), or were released in (dates), the infestations

Locality	Grid reference	<i>T. lativentre</i>	<i>R. marginatus</i>	<i>N. quadrivittatus</i>
A	33°33'S 19°12'E	(1987)		
B	28°20'S 30°02'E	(c. 1980)		
C	33°26'S 19°14'E	(1987)		
D	28°45'S 29°50'E	(c. 1980)	18 Nov. 1984	
E	32°58'S 27°49'E	(c. 1981)	31 Oct. 1984	
F	28°21'S 30°03'E	(c. 1980)	17 Jan. 1990	
G	33°03'S 27°50'E	(c. 1981)		28 Jan. 1985
H	25°02'S 31°10'E	20 May 1988		20 May 1988
I	24°50'S 28°20'E	(1986)		25 Feb. 1986
J	33°19'S 19°04'E	15 Mar 1985		13 Apr. 1988
K	33°24'S 18°59'E	(1987)		24 Oct. 1987
L	33°41'S 19°25'E	23 Aug 1985		01 Apr. 1987
M	24°28'S 28°33'E	(1987)	21 Dec. 1988	09 Nov. 1988
N	29°29'S 30°15'E	(c. 1980)	24 Nov. 1988	27 Jan. 1987
O	33°45'S 24°35'E	(1985)	10 Dec. 1987	15 Apr. 1987
P	32°05'S 18°49'E	(1987)	22 Dec. 1986	22 Dec. 1986

Table 2 Regression statistics for changes with time in the density of *Sesbania punicea* (values in Fig. 1 transformed to \log_{10} of value + 1)

Combination of agents present	Site	r^2	Slope	t -value	df	P
<i>T. lativentre</i>	A	21%	-0.011	1.26	7	0.26
	B	60%	-0.013	2.12	4	0.12
	C	53%	-0.016	2.14	5	0.10
	A-C	4%	-0.008	0.83	17	0.42
<i>T. lativentre</i> <i>R. marginatus</i>	D	44%	-0.012	1.55	4	0.22
	E	84%	-0.037	5.16	6	0.004
	F	2%	0.003	0.01	4	0.82
D-F		24%	-0.016	2.19	15	0.045
	<i>T. lativentre</i> <i>N. quadrivittatus</i>	G	4%	0.005	0.47	6
H		85%	-0.030	5.73	7	0.001
I		23%	-0.013	1.35	7	0.22
J		72%	-0.050	3.63	6	0.015
K		31%	-0.025	1.48	6	0.197
L		56%	-0.026	2.24	5	0.088
G-L		31%	-0.024	4.24	41	0.0001
<i>T. lativentre</i> <i>R. marginatus</i> <i>N. quadrivittatus</i>		M	74%	-0.044	3.75	6
	N	90%	-0.026	5.31	4	0.013
	O	60%	-0.049	2.73	6	0.041
	P	93%	-0.057	9.15	7	< 0.0001
	M-P	58%	-0.044	5.91	25	< 0.0001

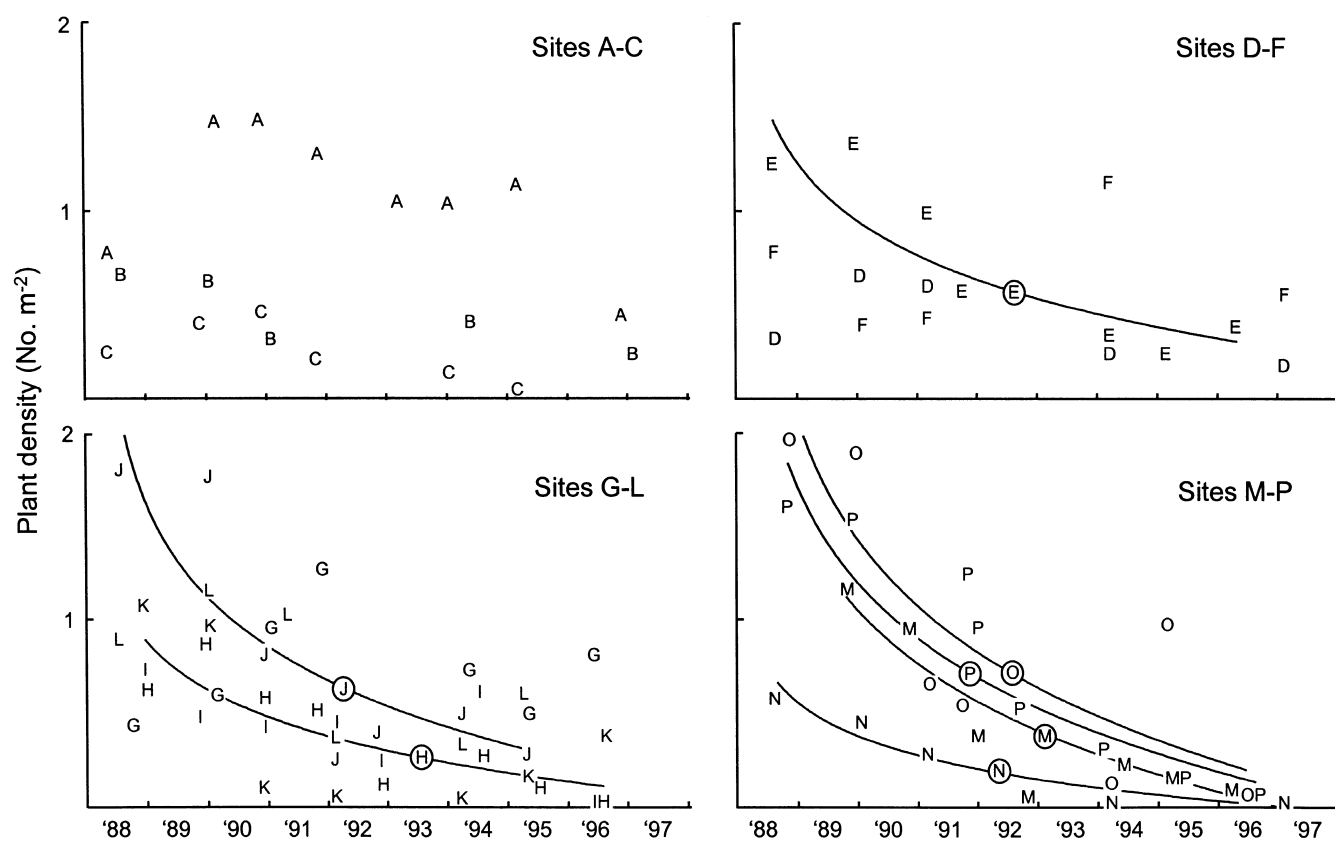


Fig 1 The mean density (number m^{-2}) of mature *Sesbania punicea* plants at sites subjected to attack over a 10-year period by three species of weevils, in different combinations. Sites A-C, *Trichapion lativentre* alone; sites D-F, *T. lativentre* and *Rhysomatus marginatus*; sites G-L, *T. lativentre* and *Neodiplogrammus quadrivittatus*; sites M-P, all three weevil species together. Regression lines have been fitted to show the trends at seven sites (identified by circled letters) where there was a significant change in the density of the weed with time (see Table 2)

of the three sites observed, and there was a significant decline in the overall density of the weed (i.e. with the results from sites D-F combined).

In combination, *T. lativentre* and *N. quadrivittatus* induced a significant reduction in the density of mature *S. punicea* plants at two out of the six sites (sites H and J) and there was a highly significant decline in the

overall density of the plants (i.e. with the results from sites G–L combined). In each of the four *S. punicea* infestations where the three weevil species, *T. lativentre*, *R. marginatus* and *N. quadrivittatus* acted in combination over the 10-year period, there was a significant decline in the density of the mature plants (sites M–P) and there was a highly significant decline in the overall density of the plants.

The large increase in the density of plants measured at site O during 1995 followed a flood in the area during 1992. The flood waters brought seeds into the area from upstream infestations of the weed and scarified the river banks which created ideal conditions for seed germination. In response to this resurgence of the weed, the land-owner cleared the infestation mechanically so that for the 1996 sample there was a marked decline in the density of plants at site O.

At two of the sample sites (F and G) there were considerable fluctuations in the density of plants with time (as shown by the low r^2 values in Table 2). Both of these sites were situated in the summer rainfall regions of the country and were adjacent to grass pastures which were burnt at least every 2 years. It seems likely that when smoke from these fires permeated the *S. punicea* infestations, *T. lativentre* and *R. marginatus* were driven from the plants and dispersed. The weevil-free plants were then able to set large numbers of seeds which in turn produced periodic pulses of recruits and caused the density of plants to fluctuate considerably. A regression analysis of the change of the overall density of *S. punicea* at the sites where *T. lativentre* and *R. marginatus* were active together, but with site F excluded, increased the significance of the regression ($r^2 = 50\%$; slope = -0.024 ; $t = 3.16$; $P = 0.01$).

Discussion

These results on the long-term effects of three introduced weevils species on the population dynamics of the woody weed, *S. punicea*, need to be placed in perspective.

Insect herbivores and plant population dynamics

There are many studies that report on the fluctuations in numbers of insect herbivores and on the performance of their host plants over time. Crawley (1983) has reviewed this topic and he has made the telling point that: "It is one thing to show that herbivorous insects affect plant performance. It is an entirely different matter to demonstrate that insect herbivores affect plant population dynamics" (Crawley 1989).

Weed biological control has probably contributed more than is generally realised to knowledge on the effects of insect herbivores on plant populations. However, the present study is the first, as far as we know, that illustrates the long-term effects of insect herbivores on

the population dynamics of a moderately long-lived tree species.

How many and what combinations of insect herbivore species are needed to reduce the density of weedy plant species?

This question in itself is almost trivial because the answer differs for each insect-plant association. For example, there are many cases from the biological control literature where one or two species of herbivores have been sufficient to suppress weed populations (Dodd 1940; Rees 1977; Goeden and Ricker 1981; Room et al. 1985) but there are other cases, such as with *Lantana camara*, where several different species of insects have not significantly affected populations of the host (Cilliers and Neser 1991).

Harris (1981, 1984) has hypothesised that successful biological control is achieved through accumulative "stress" on the host plant and that the more herbivorous species that are introduced, the greater the stress on the target weed. Myers (1985) has challenged this proposal, pointing to the frequent successes (i.e. reductions in host-plant density) achieved by a single agent and has suggested that each introduction of a new agent species is a "lottery" as regards its chances of reducing the density of the host plant.

Our results on *S. punicea* indicate the ultimately obvious point that it is what the agents do to the host plant (the quality of attack rather than the quantity of insect herbivore species) and the combination of the actions of different agents that holds the key to reductions in host-plant population densities and thus to success or failure in biological control.

The three weevil species introduced against *S. punicea* in South Africa have reduced populations of the weed to levels where it is now almost irrelevant as an invasive plant. This was achieved by the agents acting together and probably would never have been achieved by any one of the three agents acting on its own. Certainly *T. lativentre* alone was unable to reduce the density of mature *S. punicea* plants in South Africa. Although it was not possible to measure the effect of either *R. marginatus* or *N. quadrivittatus* alone on the population dynamics of *S. punicea*, evidence from simulation models (Hoffmann 1990) and from manual clearing operations supports the contention that neither agent on its own would cause a decline in the density of the weed. The simulation models show that a 84% destruction of seeds that would be expected with *R. marginatus* alone is insufficient to cause declines. This is confirmed by the fact that the much higher level (98%) of reduction in seed set caused by *T. lativentre* was also unable to reduce the density of the host plant.

The simulation models also show that when the large *S. punicea* trees in a population are destroyed, as is done by *N. quadrivittatus*, and neither *T. lativentre* or *R. marginatus* is active, the weed population is rapidly

replenished from seedlings that are produced by the substantial, though relatively short-lived (3–4 years; Graaff and van Staden 1984), reserves of seeds in the soil. The outcome is akin to that which was experienced during mechanical clearing of the weed prior to the introduction of *T. lativentre* and *R. marginatus*: mechanical removal of *S. punicea* plants was rapidly followed by a proliferation of seedlings and recruitment of new plants into the population so that cleared areas had to be continually re-cleared. Following the establishment of *T. lativentre* and *R. marginatus* in South Africa, mechanical clearing operations against *S. punicea* have been much more successful because very few seedlings are produced from the impoverished seed-bank in the soil and, once an area is cleared, minimal effort is required to keep the weed from becoming re-established.

Our experience with *S. punicea*, and with other long-lived woody weeds, such as *Prosopis* species (Zimmermann 1991), shows that satisfactory control of perennial weeds will probably seldom be accomplished by a single species of agent that drastically reduces the fecundity of its host plant. Nevertheless, this type of agent can curb the invasiveness of the weed and certainly play an essential role in reducing the density of populations of the weed when used in conjunction with other types of agents or other control methods. We advocate 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.

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