A review of recent efforts at biological control of *Caesalpinia decapetala* (Roth) Alston (Fabaceae) in South Africa

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A seed-feeding beetle, *Sulcobruchus subsuturalis* (Pic) (Coleoptera: Chrysomelidae: Bruchinae), was released in South Africa in 1999 as a biological control agent against the invasive, leguminous, scrambling shrub *Caesalpinia decapetala* (Roth) Alston (Fabaceae). Despite being easy to rear in the laboratory and having been released in large numbers (>350 000) and widely distributed at many field sites, the beetle remains scarce where present and has failed to persist at many of the original release sites. Although eggs are oviposited readily on loose seeds in dishes, the few eggs that were found at release sites in the field were always on seeds still attached to pods hanging on plants. High levels of predation and parasitism were recorded in the field, which may be hindering population expansion by the beetle. Clarity about the taxonomic status of *S. subsuturalis,* and uncertainty as to the centre of origin of the weed, have led to suspicions that *C. decapetala* may exist as several biotypes, and that the local variety may not be a suitable host for the form of *S. subsuturalis* that has been imported into South Africa. These uncertainties should be addressed, together with additional efforts to determine what is happening to the agent in the field. Other phytophagous species from different feeding-guilds need to be investigated as potential biological control agents.

Key words: Bruchinae; Mauritius thorn; seed bank; seed-feeding agent; *Sulcobruchus subsuturalis*.

INTRODUCTION

This paper is a review of attempted biological control of the invasive, climbing weed *Caesalpinia decapetala* (Roth) Alston (Fabaceae) in South Africa, mostly reporting on efforts to use a seed-feeding beetle, *Sulcobruchus subsuturalis* (Pic) (Coleoptera: Chrysomelidae: Bruchinae) (Kalibbala 2005, 2008). Several seed-feeding biological control agents have been used in South Africa for biological control of different perennial alien weed species, with some notable successes (Dennill *et al.* 1999; Gordon 1999; Hoffmann & Moran 1999; Impson *et al.* 1999; for an overview see Moran *et al.* 2004), so expectations were high that some success would be possible using this approach against *C. decapetala*.

Because *C. decapetala* can form an impervious natural barrier, it has been widely distributed throughout large parts of the paleotropics for use as a living fence. However, the negative consequences of this transformer species (Henderson 2001) far outweigh its usefulness. Uncontrolled spread of *C. decapetala* over large areas of South Africa prompted the Agricultural Research Council-Plant Protection Research Institute (ARC-PPRI), in 1988, to consider biological control as an option, the plant having been in South Africa for well over a century before that.

The biological control programme against *C. decapetala* was reviewed by Coetzer & Neser (1999), in the same year that *S. subsuturalis* was cleared for release. Since then *S. subsuturalis* has been reared in large numbers and widely distributed to many sites in at least four of South Africa's nine provinces. To date the anticipated impacts have not materialized, largely because *S. subsuturalis* has failed to proliferate at any of the original release sites and has disappeared completely from many. Nevertheless, a summary of the programme so far is presented here to provide a benchmark for future studies on the use of *S. subsuturalis* on *C. decapetala* and to guide the selection of alternative agents for future releases against *C. decapetala* in South Africa.

THE TARGET PLANT

Caesalpinia decapetala (Fig. 1) is a thorny, perennial, evergreen woody shrub which can grow to 10 m

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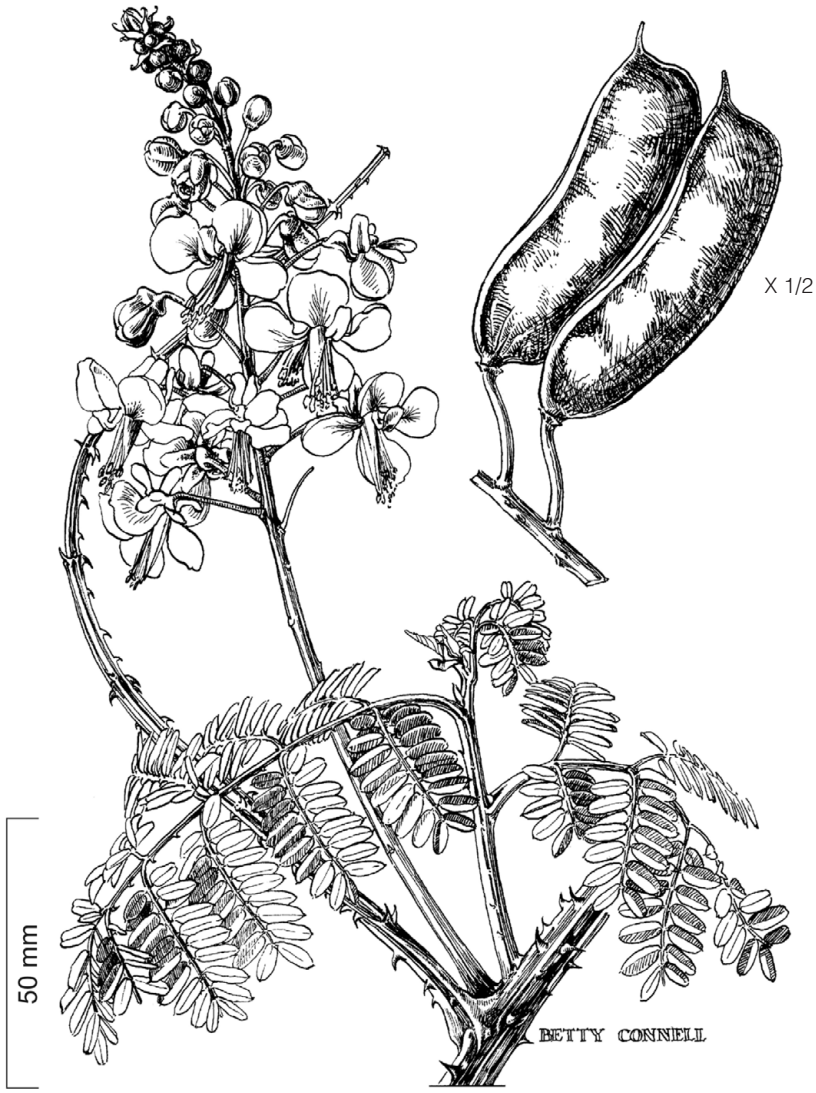

Fig. 1. *Caesalpinia decapetala*. (Drawn by B. Connell; first published in Henderson (1995), ARC-Plant Protection Research Institute, Pretoria.)

by scrambling over other vegetation (Henderson 1995). The stems are covered in prickles, as are the lower axes of the leaves which are bipinnate (twice compound), with 4–11 pairs of pinnae, having 8–13 pairs of leaflets. It is one of approximately 100 tree or shrub species in the genus *Caesalpinia* L., which in their native range grow in tropical and subtropical savannas and forests of China, Japan, Malaysia and India, and in lowland rainforest in New South Wales, Australia (Polhill & Vidal 1981; Starr *et al.* 2003). *Caesalpinia rostrata* N.E.Br is a South African indigenous, ecological analogue of *C. decapetala* (Schmidt *et al.* 2002), but none of its phytophagous fauna seems to be able to use the invading species as a host.

Although Coetzer & Neser (1999) provide an extensive description of its current distribution, the centre of origin of *C. decapetala* remains unknown. The type specimen was collected in India (Alston 1931) but this may not be part of the native range because the plant has been widely utilized as a natural fence throughout India, Indochina, China, Japan, Korea, and Malesia (which is the biogeographical region straddling the indo-Malaysian

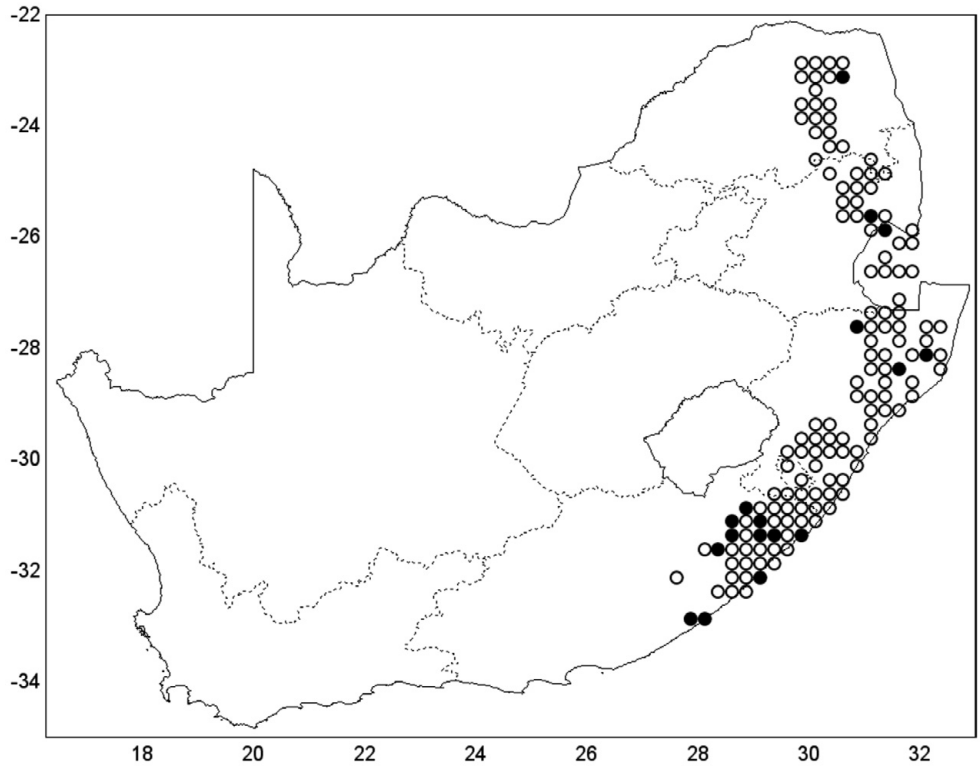

Fig. 2. Distribution of *Caesalpinia decapetala* in South Africa. ● = quarter degree squares recorded since 2000, many in the Eastern Cape, which was not well surveyed in the past. Most new records are from a helicopter survey conducted in 2004, which should be regarded as densification of *C. decapetala* rather than spread to new sites (L. Henderson, pers. comm.). (Drawn by L. Henderson; data source: SAPIA database, ARC-Plant Protection Research Institute, Pretoria.)

archipelago and northern edge of Australasia) (Hattink 1974; Saldanha & Gurudev Singh 1984; Hou *et al.* 1996).

The relatively depauperate insect fauna collected on *C. decapetala* in India, notably a lack of primary stem borers and gall formers, provides further evidence that India is not within the natural distribution of the plant (Coetzer & Neser 1999). Coetzer & Neser (1999) concluded that Indonesia and Malesia could be near the centre of origin but surveys for natural enemies in Sumatra were unsuccessful (Coetzer 2000a). Difficulties in searching for natural enemies have been compounded by the inconsistent taxonomy of the genus (Coetzer & Neser 1999), and by its morphological variability, which led Isely (1975) to recognize two distinct varieties; *C. decapetala* var. *decapetala* and *C. decapetala* var. *japonica,* depending on geographical origin and chromosome number. The possibility that there are different biotypes of *C. decapetala* could explain the lack of success of the one biological control agent released against it in South Africa in 1999.

Introduction, distribution and weed status in South Africa

Caesalpinia decapetala has become invasive on Raoul Island, New Zealand (Devine 1977) as well as in Australia, the U.S.A., East Africa (Kenya) and Zimbabwe (Holm *et al.* 1991) and it is widespread in South Africa (Fig. 2) (Henderson 1995). In South Africa it is commonly known as 'Mauritius thorn', or 'Kraaldoring' in Afrikaans. It was first recorded in Durban, in KwaZulu-Natal Province (KZN) in 1888 and may have already been widespread by 1899 (Coetzer & Neser 1999). As in many other countries, it has been grown in South Africa as a natural fence, alongside numerous other indigenous thorny species (Coetzer & Neser 1999).

The invasive potential of *C. decapetala* has been recognized in South Africa since the 1960s, but it was only officially declared a weed in 1983

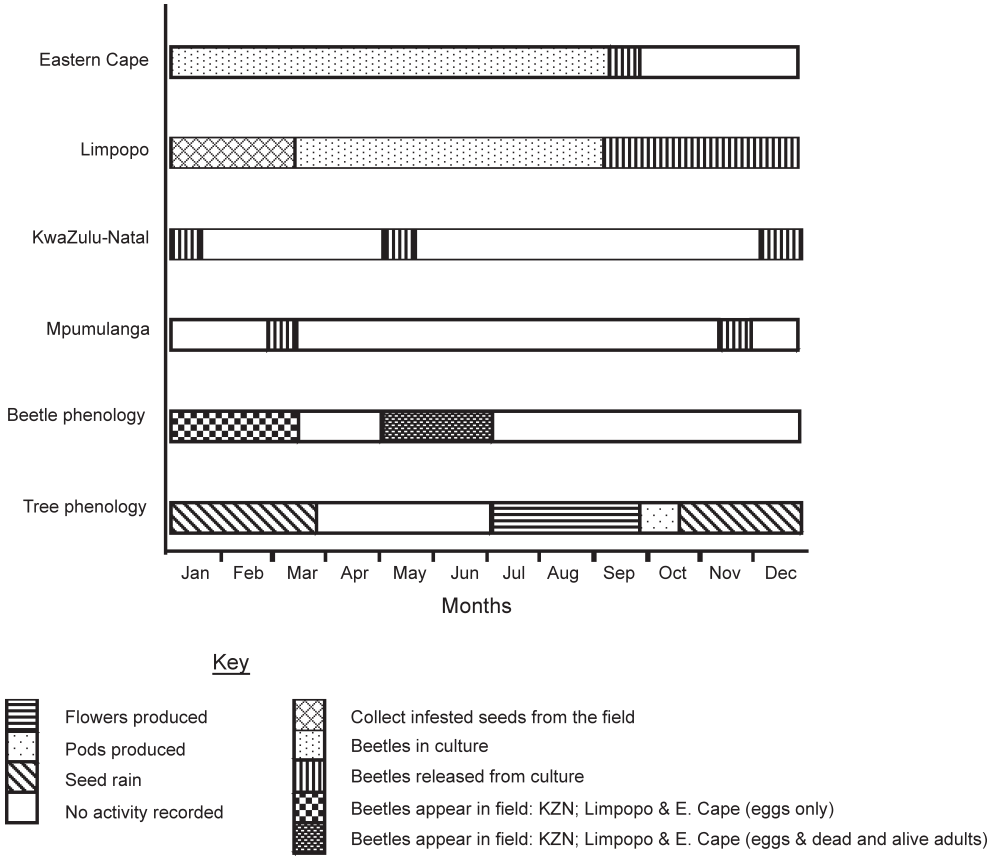

Fig. 3. Mass-rearing and release of *Sulcobruchus subsuturalis* by province, and the phenology of the beetle and its host, *Caesalpinia decapetala*, recorded in the field in KwaZulu-Natal Province, unless otherwise indicated in the key.

(Coetzer & Neser 1999). Today, the plant threatens agriculture by occupying grazing land and injuring livestock (Henderson 2001). It invades commercial plantations of timber and tropical fruit orchards, natural areas such as riparian vegetation, forest margins and savannas in the moist eastern parts of the country (Coetzer 2000b). It increases fire risk. In native subtropical forests it causes trees to collapse and shades out understorey plants (Geldenhuys *et al.* 1986). It may also be able to fix nitrogen, and could therefore alter soil nutrient balance, as happens with other invasive leguminous species (Witkowski & Mitchell 1987; Witkowski 1991a; Drake 2011). The weed has an almost unbroken distribution from the north of Limpopo, extending southwards across Mpumalanga, the neighbouring country of Swaziland, and KZN and almost half way across the Eastern Cape Province in the south (Henderson 2001). By 1998, *C. decapetala* was ranked number 20 out of a total of 25 invader species in South Africa in terms of its water use, which was estimated to be 33.82 million m^3 per annum (Versfeld *et al.* 1998).

Biology and ecology

Caesalpinia decapetala bears pale yellow flowers which are pollinated by various insect species. The flowers are produced in long racemes (Fig. 3) over an extended period starting in winter (July) and peaking in spring (September) (Kalibbala 2008) and give rise to ellipsoid, large dark brown seeds (8 × 6 mm) in woody leguminous seed pods, from spring and throughout summer (up to March) (Kalibbala 2008). Most seed pods dehisce and release their seeds while still in the canopy, but some intact pods still containing seeds fall to the ground where they persist for up to a year. Seed rain occurs from mid-October to April with up to 400 seeds/m^2 accumulating under the plant canopy, declining to about 100 seeds/m^2 a short

distance (10 m) beyond the canopy edge (Kalibbala 2008). Its prolific reproductive output undoubtedly accounts for the colonization potential of *C. decapetala* in many parts of the world (Lake & Leishman 2004).

The seeds have a hard seed coat, typical of many legumes. Scarification or acid treatment reduces the time taken to germinate, and increases the percentage of seeds that germinate within 30 days from about 80 % to almost 100 % (Witkowski 1991b; Teketay 1996). The seed coat is reputed to allow *C. decapetala* seeds to remain viable in the soil for several years (West 2002) but there are no quantified measurements to support this claim. In general, the seed bank appears to be largely ephemeral, as seed numbers in the soil decline rapidly through the year. At Boughton, KZN (S29°36′10.0″ E30°19′43 10″) where the plants failed to flower during summer 2006 because of herbicide damage, a decline to 11 seeds/m^2 was recorded under the canopy by February 2008, a year after the previous flowering event (Kalibbala 2008). This record showed that some seeds can persist in the soil for at least one year and hence *C. decapetala* has at least a short-term persistent seed bank. Additional support for seed longevity is the presence of seeds at depth in the soil, a position they would be unlikely to reach in a short period. The causes of seed bank decline are unknown.

Germination is induced by rainfall. A maximum of 70 seedlings/m^2 was recorded under the canopy in summer at Ferncliffe, KZN (S29°33′55.2″ E30°19′51.7″). None of these seedlings survived during winter, presumably through lack of water because the site was undisturbed (Kalibbala 2008; Wilson & Witkowski 1998). Vegetative propagation is common with new plants forming from branches taking root where they touch the ground (adventitious rooting). This process makes it difficult to distinguish individual *C. decapetala* plants, and hence to assess the age (or size) class and to estimate the longevity of individual plants. The minimum age or size for reproductive maturity is unknown.

Mechanical and chemical control

The herbicides registered for use against *C. decapetala* are listed in Vermeulen *et al.* (1998). Effective control requires both chemical and mechanical methods, where the herbicides are applied to young plants and to the re-growth of slashed mature plants (Bromilow 1995). A combination of herbicidal and mechanical control of the weed has been successful on Raoul Island, New Zealand (West 2002), which represents a special case of a small, confined area with a great variety of resources being utilized to achieve success. The growth form of *C. decapetala* in South Africa makes it particularly difficult to control because the strong recurved prickles impede access into infested areas. It cannot be sprayed without damaging non-target plants because it grows in the mixed canopy and must therefore be slashed first which is difficult in inaccessible areas such as steep river banks. Cut stumps coppice strongly and new plants form where stems produce adventitious roots as they intermingle with neighbouring shrubs and trees. Control is only possible provided regular follow-up foliar herbicide applications are applied. For mechanical control to be effective, the whole root system must be excavated at great cost (Bromilow 1995). Finally, new plants also establish from seeds banks, exacerbating the difficulties of control.

Biological control

Biological control of *C. decapetala* offers a less damaging, alternative management mechanism (Neser & Annecke 1973), but has been constrained by a lack of suitable natural enemies. A company (BioControl Research Laboratories) was commissioned to search for insects associated with *C. decapetala* in India, and produced a list of 41 species. Amongst the collection were six specimens of *Sulcobruchus bakeri* Kingsolver (Coleoptera: Chrysomelidae: Bruchinae) and six specimens of the moth, *Acrocercops hyphantica* Meyrick (Lepidoptera: Gracillaridae) (Manjunath *et al.* 1992). *Sulcobruchus bakeri* is a synonym of *S. subsuturalis* (Anton 1999). Specimens of the bruchine beetles were sent to the British Museum (Natural History) and subsequently identified by J.M. Kingsolver.

Sulcobruchus subsuturalis was collected in seeds of *C. decapetala* in 1996 by S. Neser and C. Zachariades of the ARC-PPRI, from a site in Karnataka State, called Byatrayanapura, near Bangalore (12.58N 77.35E), and three other sites in Maharashtra State, near the Nira River (18.09N 74.02E), near Pune (18.34N 73.58E) and at Wai (17.57N 73.57E) (Coetzer & Neser 1999). From these collections, and starting with the adult beetles that emerged from all these seeds, a single quarantine culture was established at the quarantine facility of the ARC-PPRI in Pretoria (Coetzer &

Neser 1999). After extensive host-specificity testing (Coetzer 2000b), permission for release of *S. subsuturalis* was granted in 1999, and by November 2000 more than 60 000 adults had been released (Hill 2000).

The leaf-mining gracillariid moth, *A. hyphantica,* was collected in India in 1998 for introduction into quarantine in South Africa. It was envisaged that this species might defoliate the *C. decapetala* plants and, in addition to seed destruction by *S. subsuturalis,* might help to suppress populations of the weed. A single *A. hyphantica* larva can destroy 3–4 leaflets, after which it pupates in a cocoon on the upper surface of an undamaged leaflet (Coetzer & Neser 1999). Despite early optimism about its host specificity (Coetzer & Neser 1999), this was not borne out by laboratory trials during which *A. hyphantica* laid eggs on *Cassia abbreviata* Oliv., *Ceratonia siliqua* L., *Caesalpinia ferrea* Martius and *Sophora inhanbanensis* Klotzsch (Fabaceae) (W. Coetzer, ARC-PPRI, unpubl.). *Acrocercops hyphantica* has also been reported to develop on *Caesalpinia bonduc* (L.) Roxb. (Fletcher 1993), although no oviposition was recorded on this species (Coetzer 2000a). The moth was never released from quarantine and all research on it was terminated in 2000 (Hill 2000).

Two other insect species that are considered to have some potential as agents are the bud-feeding weevils, *Amorphoidea* sp. and *Endaeus* sp. nr *butae* (Coleoptera: Curculionidae). No attempt has yet been made to rear either of these species in quarantine (Coetzer 2000a).

The combination of a successful laboratory culture of the seed-attacking *S. subsuturalis,* and the perception that *C. decapetala* was spread largely through prolific seed production, led to this seed-feeding beetle being considered as the most promising biological control agent.

THE SEED-FEEDING BRUCHINE, *S. SUBSUTURALIS*

Taxonomy and biology

Besides being found in *C. decapetala* seeds at several sites in India (Manjunath *et al.* 1992; Coetzer & Neser 1999; Coetzer 2000b), *S. subsuturalis* has also been recorded from other hosts in India, including, *Dalbergia candenatensis* (Dennst.) Prain (Papilionaceae) and *Moullava spicata* (Dalz.) Nicolson (Caesalpiniaceae) (Anton 1999). Anton (1999) synonymized *S. subsuturalis* with three other bruchine species, which all have widely separated oriental type-localities, but he only reported on the host plants from India, as above. The type locality of *S. subsuturalis* is Banggi Island, northeast of Sabah, Kalimantan (formerly Banguey Island, Borneo). It has also been collected in Thailand (Anton 1999). Along with the question of the centre of origin of *C. decapetala,* the apparent oligophagy of *S. subsuturalis* raises uncertainties, including whether *C. decapetala* is among the beetle's regular hosts or whether the beetle is a mix of cryptic species each associated with a specific host. Coetzer (2000b) showed that in the laboratory, the provenance of *S. subsuturalis* which was introduced into South Africa oviposited readily on seeds of *C. decapetala*. Coetzer (2000b) assumed that *S. subsuturalis* adults overwinter within the dehisced *C. decapetala* pods.

In the laboratory, *S. subsuturalis* only lays eggs on *C. decapetala* seeds when they are presented uncovered in closed containers such as Petri dishes. In cages, very few eggs were laid on seeds placed on the soil surface and even fewer on seeds in pods suspended above the soil. Coetzer (1998) also noted that *S. subsuturalis* preferentially laid eggs on exposed seeds in choice- and no-choice tests. No eggs are laid on seeds buried 2 or 4 cm, respectively, below the soil surface (Kalibbala 2008). This behaviour pattern raises suspicions that *C. decapetala* is not the preferred host *of S. subsuturalis* because the beetles reject seeds when they are most readily available, *i.e.* scattered on the soil surface.

When *S. subsuturalis* larvae complete their development and eclose as adults, seed germination rates drop to about 10 % of those of intact seeds (Kalibbala 2008), showing that the beetle has the potential to substantially reduce the reproductive capacity of the plants. Besides these observations, little is known about the biology of *S. subsuturalis* in relation to *C. decapetala*.

Mass-rearing and release

Working on the assumption that agents in their new habitat will reproduce freely on their superabundant weed hosts, insufficient release effort prevails and is often blamed for poor agent establishment or failure (Grevstad 1999). This accusation cannot be levelled at the release programme of *S. subsuturalis* against *C. decapetala* in South Africa, where more than 350 000 beetles were released at 233 sites between 2000 and 2006

Table 1. Sites at which *Sulcobruchus subsuturalis* was released for biological control of *Caesalpinnia decapetala* and then later selected for post-release evaluation of the beetle. Data sourced from the ARC-PPRI and WfW records.

Site Name	Province	Coordinates		Date of last release of agents	No. agents released on last occasion
Bodupe	Limpopo	S23°39′19.7″	E30°15′49.4″	12 Dec. 2006	17 500
Moshakga 1	Limpopo	S23°39′34.3″	E30°15′55.6″	21 Dec. 2002	20 500
Moshakga 2	Limpopo	S23°39′42.0″	E30°15′09.0″	31 Dec. 2002	19 000
Nelsriver Bridge	Mpumalanga	S25°25′52.8″	E30°58′03.8″	14 Mar. 2005	1 000
Riverwild	Mpumalanga	S25°20′19.0″	E30°38′37.7″	19 Nov. 2002	1 000
Tropicado	Mpumalanga	S25°19′32.5″	E30°41′51.9″	19 Nov. 2002	2 000
Boughton	KwaZulu-Natal	S29°36′10.0″	E30°19′43.1″	03 Jan. 2003	2 000
Ferncliffe	KwaZulu-Natal	S29°33′55.2″	E30°19′51.7″	14 May 2001	900
Mtubeni Valley	KwaZulu-Natal	S29°33′59.9″	E30°06′44.0″	30 Dec. 2003	1 917
Nomvalo	Eastern Cape	S31°31′19.3″	E29°32′23.0″	28 Sep. 2005	4 800
Tutor-Ngeleni pass	Eastern Cape	S31°34′46.6″	E29°13′11.6″	28 Sep. 2005	4 800
Tutor-Ndamase pass	Eastern Cape	S31°34′54.0″	E29°13′11.6″	28 Sep. 2005	4 800
Overall	12 major releases	Latitudinal range = 8°	Longitudinal range = ~2°	May 2001 – Dec. 2006	80 217

(Kalibbala 2008). This impressive record was probably the result of a fortuitous coincidence that the beetles were easy to breed in the laboratory on seeds of *C. decapetala* collected from the field, and that mass-rearing facilities were set up at that time, by the *Working for Water* Programme (WfW) of the Department of Water Affairs, for a range of species of biological control agents. A summary of releases recorded by the ARC-PPRI up to 2006 is given in Table 1. More details of these releases are given by Kalibbala (2008).

Generally, in the Eastern Cape, beetles were reared between January and August to obtain sufficient numbers for releases in September (early spring/summer) (Fig. 3). However, releases have also been made in February and June (C. Zachariades, ARC-PPRI, pers. comm.). In Limpopo, infested seeds were collected from the field between January and March to provide stocks of beetles for mass-rearing indoors between April and November for releases during September and December. Soon after beetles were released in the field, the quarantine colonies were destroyed to eliminate rising numbers of itch mites (Acari), which irritated workers and killed the beetles developing in the seeds. In KZN, releases took place in May 2001, January 2003 and December 2003. In Mpumalanga releases took place in November 2002 and March 2005. More often than not, releases were undertaken in summer when the beetles were expected to be reproductively active and when mature seeds were available on the plants (spring through to summer) (Fig. 3). Releases of *S. subsuturalis* have continued in Limpopo, with more than 14 000 adults being distributed between seven sites since 2005 (D. Strydom, WfW, pers. comm.).

Evidence of establishment

During the later stages of the release programme, from 2005–2007, the Capacity Building Programme of WfW, supported a post-release evaluation of *S. subsuturalis* on *C. decapetala,* to examine the establishment and impact of the bruchines at selected sites in four provinces (Table 1). Field work was conducted over 15 months (February 2006 to April 2007).

Seven of the 12 study sites showed signs of *S. subsuturalis* damage with the highest percentage of seeds affected reaching 15.5 % at one site (Table 2). Most indications of the presence of *S. subsuturalis* were from hatched eggs, all of which were found adhering to seeds still within pods on the plants. The numbers of eggs recovered per site was related to the numbers of beetles last released at the site ($R^2 = 0.519$, $P = 0.018$). The adults recovered were usually found as dead individuals inside seeds collected from pods still on the plant in winter, and were not related to the numbers of adults released on the last occasion ($R^2 = 0.004$, $P = 0.861$). Live adults were only found in collections from Limpopo Province (Table 2). No seeds with larvae, or adult exit holes were found. The recoveries were not from seeds

Table 2. Recovery of *Sulcobruchus subsuturalis* eggs or adults in seeds collected from pods in the canopy at sites where the agent was released for biological control of *Caesalpinia decapetala*. Site location, and date and number of last release are given in Table 1.

Site Name	Province	Sample date	Number of seeds sampled	Seeds bearing eggs *n* (%)	Seeds with adult beetles *n* (%)	Eggs parasitized *n* (%)
Bodupe	Limpopo	Jun. 2007	374	24 (6.4)	2 (0.53)	18 (75)
Moshakga 1	Limpopo	Jun. 2007	214	29 (13.6)	3 (1.4)	24 (82)
Moshakga 2	Limpopo	Jun. 2007	103	16 (15.5)	1 (0.97)	15 (93)
Nelsriver Bridge	Mpumalanga	Feb. 2007	33	0 (0)	0 (0)	0 (0)
Riverwild	Mpumalanga	Feb. 2007	144	0 (0)	0 (0)	–
Tropicado	Mpumalanga	Feb. 2007	333	0 (0)	0 (0)	–
Boughton	KwaZulu-Natal	May 2005	179	1 (0.6)	1 (0.56)	0 (0)
Ferncliffe	KwaZulu-Natal	May 2005	90	0 (0)	0 (0)	0 (0)
Mtubeni Valley	KwaZulu-Natal	May 2005	22	3 (13.6)	2 (9)	0 (0)
Mtubeni Valley	KwaZulu-Natal	Jan. 2007	210	1 (0.5)	0 (0)	0 (0)
Nomvalo	Eastern Cape	Feb. 2007	224	10 (4.5)	0 (0)	0 (0)
Overall	10 sites	4 dates	1926	96 (4.9)	21 (1.1)	30 (31)

that had been strewn on the ground during releases from the mass-rearing cultures, because beetles and eggs were only found on seeds in pods still in the canopy.

These observations indicate that the beetles are reproducing in the field, but in very low numbers, at a limited number of sites.

Predation and parasitism

Predators or parasitoids could be factors constraining the agent. It is well known that biological control agents are often attacked by native predators and parasitoids after their release from quarantine (Hill & Hulley 1995; Cornell & Hawkins 1993; Olckers 1995; Paynter *et al.* 2010) and predation by ants is particularly common (Robertson 1985, 1988). When eggs were taken from laboratory cultures and placed on the ground in the field, 100 % were removed by predators within six days, well within the incubation period of approximately eight days (Coetzer & Neser 1999). In experiments where the eggs were protected from ants, up to 60 % were removed by other unknown predators. Within 12 days, in the field, predators had also removed all adult beetles preparing to emerge from the seeds, and ants were found inside the hollow seeds (Kalibbala 2008).

The immature stages were also subjected to parasitism by wasps (Hymenoptera: Pteromalidae) (Kalibbala 2008), which agrees with records for other bruchine populations in the field (Hetz & Johnson 1988; Impson *et al.* 1999). Of the few *S. subsuturalis* eggs that survived predation in the field, up to 90 % had an emergence hole on the upper surface of the shell, indicative of parasitism by wasps (possibly Hymenoptera: Trichogrammatidae), while eggs at some of the sites showed no evidence of parasitism (Table 2).

DISCUSSION

Caesalpinia decapetala remains a pernicious invader in South Africa. It was specifically targeted as one of 18 species for manual-clearing by WfW in the riparian areas of Mpumalanga Province (Garner & Witkowski 1997). Along the Sabie River riparian fringe in Mpumalanga alone, the density of *C. decapetala* has greatly increased since 1996/1997. From low levels in a few plots, where it was largely suppressed by shading from *Eucalpytus grandis* W. Hill ex Maiden (Myrtaceae), it attained a mean of 400 plants/ha by 2005 after *E. grandis* had been removed (Beater 2006; Beater *et al.* 2008). The homogenizing effects of a 1-in-75-year flood during 2000, aided the spread of numerous alien plant species, including *C. decapetala,* in Mpumalanga (Witkowski & Garner 2008). The range-expansion of *C. decapetala* has occurred despite WfW clearing efforts in the intervening years.

Surprisingly, an extensive general soil seed-bank study undertaken in 1996/1997 (Garner 2006; Witkowski & Garner 2008) did not identify any *C. decapetala* seeds, although this may be an artefact: the seeds collected during the survey

were identified by officials of the Directorate of Plant and Quality Control, National Department of Agriculture in 1997 and all the seeds that were found in low numbers were categorized as 'unknown species'.

Hill (2000) recommended releases of at least 3000 adult *S. subsuturalis* beetles per site, and large numbers have been released over much of the range of *C. decapetala,* at different times of the year, which should have offset any possible climate incompatibilities (Kalibbala 2008). Further, because single *C. decapetala* seeds are capable of supporting the development of several *S. subsuturalis* individuals (Kalibbala 2005), the records may have underestimated the number of beetles released on each occasion. Despite this, no recoveries of beetles were recorded by WfW extension-officers at any site up to 2006. On one occasion, seeds with beetle emergence-holes were found, but these could have been the beetle-colonized seeds that were distributed originally.

The meagre recoveries of adult beetles made by Kalibbala (2008) are not yet clear evidence of self-sustaining populations, leading to the conclusion that the beetles have yet to reach the first benchmark of success, which is to show evidence of increasing abundance in the field (Syrett *et al.* 2000). However, the agent is easy to rear and distribute, so further releases should concentrate on one region (probably in Limpopo where live recoveries were made) with the objective of confirming, or otherwise, that a population can be established. Additional efforts should be directed to discovering why the beetles have not flourished in the field.

A mismatch between an agent's native-range plant-biotype and the introduced-range plant-biotype has caused the failure of other biological control agents (Volchansky *et al.* 1999; Charudattan 2005; Sobhian *et al.* 2003; Zachariades 2003) and cannot be ruled out as a cause of poor establishment of *S. subsuturalis* on *C. decapetala* in South Africa. An investigation of the varieties and biotypes of *C. decapetala* present in South Africa and its putative region of origin is warranted, including the collection sites of *S. subsuturalis* in India which were the provenance of the beetles that were introduced into South Africa. Because collected material of *S. subsuturalis* was all combined into one homogenous culture (Coetzer & Neser 1999) and reared on locally-collected *C. decapetala* seeds, any natural selection in the laboratory should have been for a *S. subsuturalis* population that fared best on the variety of *C. decapetala* that occurs in South Africa, thereby increasing its chances of establishment. A molecular investigation of the phylogeography of *C. decapetala* seems to be an essential step forward to find the centre of origin of the plant, and as a start in identification of possible varieties or biotypes of the bruchines.

Finally it should be borne in mind that seed-attacking biological control agents acting alone are highly unlikely to suppress the population of a weed. In combination with other agents that cause die-back of the host plant, control can be achieved (Hoffmann & Moran 1998; Moran *et al.* 2004). Thus, during further exploratory attempts focused on *S. subsuturalis,* special efforts should also be made to identify stem borers and gall formers, and other phytophages that damage the vegetative tissues of the plant, and that have the potential to supplement the potential impact of *S. subsuturalis* as a biological control agent in South Africa, should it ever become established and abundant.

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