

Impacts of a native parasitic plant on an introduced and a native host species: implications for the control of an invasive weed

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- **Background and Aims** While invasive species may escape from natural enemies in the new range, the establishment of novel biotic interactions with species native to the invaded range can determine their success. Biological control of plant populations can be achieved by manipulation of a species' enemies in the invaded range. Interactions were therefore investigated between a native parasitic plant and an invasive legume in Mediterranean-type woodlands of South Australia.
- **Methods** The effects of the native stem parasite, *Cassytha pubescens*, on the introduced host, *Cytisus scoparius*, and a co-occurring native host, *Leptospermum myrsinoides*, were compared. The hypothesis that the parasitic plant would have a greater impact on the introduced host than the native host was tested. In a field study, photosynthesis, growth and survival of hosts and parasite were examined.
- **Key Results** As predicted, *Cassytha* had greater impacts on the introduced host than the native host. Dead *Cytisus* were associated with dense *Cassytha* infections but mortality of *Leptospermum* was not correlated with parasite infection. *Cassytha* infection reduced the photosynthetic rates of both hosts. Infected *Cytisus* showed slower recovery of photosystem II efficiency, lower transpiration rates and reduced photosynthetic biomass in comparison with uninfected plants. Parasite photosynthetic rates and growth rates were higher when growing on the introduced host *Cytisus*, than on *Leptospermum*.
- **Conclusions** Infection by a native parasitic plant had strong negative effects on the physiology and above-ground biomass allocation of an introduced species and was correlated with increased plant mortality. The greater impact of the parasite on the introduced host may be due to either the greater resources that this host provides or increased resistance to infection by the native host. This disparity of effects between introduced host and native host indicates the potential for *Cassytha* to be exploited as a control tool.

Key words: Biological control, *Cassytha pubescens*, *Cytisus scoparius*, *Leptospermum myrsinoides*, parasitic plant, plant interactions, plant invasion, Scotch broom.

INTRODUCTION

Invasive species become a management problem in natural ecosystems when an increase in their distribution and abundance results in disruption to ecological processes and the emergent properties of these systems. The ability of an invader to increase into a new range depends upon the opportunities the invaded community provides for the invader and the characteristics of the invading species (Shea and Chesson, 2002). The role of biotic interactions in the invasion process has long been considered important (see, for example, Darwin, 1859; Elton, 1958) but has less frequently been addressed in empirical research.

Two hypotheses have been proposed to explain how biotic interactions influence the invasive process. The enemy release hypothesis (ERH) proposes that plants invading a new range are able to spread and increase in abundance as they escape from population regulation by their co-evolved natural enemies that occur in their native range (Maron and Vila, 2001; Keane and Crawley, 2002; Parker and Hay, 2005). In contrast, the biotic resistance hypothesis (BRH) suggests that strong biotic interactions with native competitors,

pathogens and/or herbivores in the invaded community can prevent invading species from establishing (Elton, 1958; Maron and Vila, 2001; Parker and Hay, 2005). The ERH predicts that generalist enemies in the new range will prefer native over introduced plants, and there will be no specialist enemies of the introduced plant present, thereby conferring a competitive advantage to the invading species. However, there is little empirical support for this (Maron and Vila, 2001; Agrawal and Kotanen, 2003; Colautti *et al.*, 2004; Parker and Hay, 2005; Parker *et al.*, 2006; Parker and Gilbert, 2007), as generalist enemies can have similar or greater effects on introduced species than on native species (but see Nunez *et al.*, 2008). In the case of invertebrate herbivores of plants, however, there is evidence supporting both the ERH and BRH hypotheses. Specialist herbivores can regulate plant populations in their native range, whilst in the invaded range specialist herbivores tend to be absent (ERH); however, generalist herbivores provide resistance to invasion (BRH) (Strong *et al.*, 1984; Liu and Stiling, 2006). Similar patterns have been observed for plant pathogens, with invasive and native species being equally or less susceptible to generalist pathogens (Agrawal *et al.*, 2005; Parker and Gilbert, 2007), and some evidence of escape by introduced species from specialist pathogens of their native range (Mitchell and Power, 2003).

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Classical biological control of invasive species exploits the ERH by introducing specialist enemies into the invaded range. Effective biological control agents have high host specificity and cause direct damage to the target species through continuous and prolonged attack (Myers and Bazely, 2003); however, the ecological drawbacks to this control method include the introduction of further exotic species into new ranges. If introduced species are more susceptible to native enemies than native species, then the introduction of native enemies into new populations of invading species may provide a viable control strategy (Colautti *et al.*, 2004). This strategy would have an advantage if native plants have more resistance to the native enemy than the invading species, as predicted by the BRH.

Cytisus scoparius (Scotch broom; hereafter *Cytisus*) is a leguminous shrub native to Europe that is invasive in Australia, New Zealand and North America (Syrett *et al.*, 1999). Population densities of *Cytisus* are higher in Australia than in the native range, although population longevity and plant size do not differ between the introduced and native ranges (Paynter *et al.*, 2003). Phytophagous insects significantly inhibit the growth of *Cytisus* in its native range (Waloff and Richards, 1977). Similar herbivores, however, have little impact on introduced populations in the United States (Bossard and Rejmánek, 1994), New Zealand or Australia, despite the fact that generalist phytophagous insects are common on *Cytisus* in Australia and New Zealand (Memmott *et al.*, 2000). The introduction of specialist insects from the species native range has also met with only limited success to date in invasive populations (Bossard and Rejmánek, 1994; Syrett *et al.*, 1999). The species may encounter little biotic resistance in the communities it invades, at least in Australia and New Zealand, where it is a superior resource competitor with at least some of the native shrubs with which it co-occurs (Bellingham, 1998; Fogarty and Facelli, 1999).

A new potential enemy of *Cytisus* in the temperate woodlands of southern Australia has recently been observed. The native parasitic vine, *Cassytha pubescens* (Dodder laurel; hereafter *Cassytha*), occurs at high densities on *Cytisus* and observations suggest that infection by the parasite results in damage to this host. Parasitic plants can affect host productivity by extracting water, nutrients and organic compounds from the host's vascular system and also by impacting on host physiology and thus impairing the host's ability to acquire resources (Press *et al.*, 1999). The extent to which this impacts on host performance depends upon the degree of autotrophy of the parasite, the relative ability of host and parasite sinks to attract resources (Graves, 1995; Press *et al.*, 1999) and the tolerance or resistance to infection of the host species (Koskela *et al.*, 2001, 2002; Rispaill *et al.*, 2007).

Cassytha is a stem hemi-parasite with a broad host range, although it is mostly confined to woody shrubs (McLuckie, 1924). Host-parasite associations can range from highly host-specific, to generalist, where a parasite may infect many species across taxonomic and functional groups. Most parasites display some host preference, where performance is poorer on non-preferred species and parasite density is proportional to host availability (Kelly *et al.*, 1988; Horning, 1995; Musselman and Press, 1995). Variation in the observed effects of a parasite on its host may be due to the combined

influence of the virulence of the parasite and the susceptibility of the host (Keith *et al.*, 2004). Typically, increasing negative effects of a parasite on its host are observed on host plants upon which parasites can achieve the highest biomass (Atsatt and Strong, 1970; Kelly *et al.*, 1988; Graves, 1995; Marvier, 1998; Cameron *et al.*, 2008). Hosts with a high nutrient content such as legumes are preferred hosts for several parasitic species (Matthies, 1996; Pate and Bell, 2000; Pennings and Callaway, 2002; Suetsugu *et al.*, 2008; but see Marvier, 1998). Parasite growth is often greater on nitrogen-fixing hosts (Press *et al.*, 1993; Seel and Press, 1993) but the impacts on the host are also greater (Jeschke *et al.*, 1994; Matthies, 1996; Jeschke and Hilpert, 1997).

In this study, the impacts of infection by the native parasitic plant, *Cassytha pubescens*, on a co-occurring native species, *Leptospermum myrsinoides* (hereafter *Leptospermum*), and a novel host, the introduced species, *Cytisus scoparius*, are examined. The hypothesis is tested that the parasite, as a native generalist, will have a greater impact on the novel host *Cytisus* than the native host *Leptospermum*, with which it has co-existed, and possibly co-evolved. It is predicted that the parasite will be able to achieve higher growth rates on the introduced species and will consequently have greater impacts on the physiology and growth of this species than its native host.

MATERIALS AND METHODS

Study site

The study was undertaken in the Mount Lofty Ranges of South Australia (138.69°N, 35.03°E). The study area is secondary *Eucalyptus obliqua* woodland with an overstorey of scattered *E. obliqua* trees and an understorey dominated by sclerophyllous shrubs. *Cytisus* forms dense stands in places, particularly under remnant *E. obliqua* and occurs scattered throughout regenerating native shrubs. The perennial ground layer comprises sedges, grasses and low sclerophyllous shrubs.

The climate at the study site is Mediterranean-type, with cool, wet winters and hot, dry summers. Soils are sandy loams to sandy clays with low nitrogen and phosphorous content and a pH of 5–6 (H. T. Tsang, University of Adelaide, unpubl res.).

Study species

Cassytha pubescens R.Br. (Lauraceae) is a stem-twining, parasitic vine. The plant is free-living following emergence from the seed but after approx. 6 weeks is completely dependent on a host plant for growth, survival and reproduction (McLuckie, 1924). The leaves are reduced to small scales and the photosynthetic tissue of the plant occurs in the stem. The stems branch extensively and may twine around each other or over one to several host plants. The habit and morphology of *Cassytha* are similar to the widespread parasitic genus *Cuscuta* (Convolvulaceae).

Cytisus scoparius (L.) Link (Leguminosae) is a tall, woody, short-lived shrub native to the Mediterranean region. From a supposed initial introduction to Australia in about 1800 (Waterhouse, 1988), by the mid-1800s the plant had been

introduced to most of the south-east of Australia as either an ornamental or hedging plant (Hosking *et al.*, 1996). The plant is invasive in the Mount Lofty Ranges where it occurs in disturbed woodlands in the higher rainfall areas. In these woodland systems, *Cytisus* has high rates of growth and photosynthesis in the spring months but during summer the plants lose their leaves, although the stems remain photosynthetic (Fogarty and Facelli, 1999).

Leptospermum myrsinoides Schltdl. (Myrtaceae) is a medium to tall woody, sclerophyllous shrub that occurs naturally throughout south-eastern Australia. It occurs sparsely throughout the Mount Lofty Ranges but can become dominant in more open areas of heath vegetation, particularly on sandy soils (Specht and Rundel, 1990). *Leptospermum* was selected as a native host for this study as *Cassytha* grows at high density on this species, this species occurs at similar densities as *Cytisus* at the study site (see Results), and the species has a similar growth habit to *Cytisus*. Although it would have been preferable to compare *Cassytha* impacts on a native legume with the introduced legume *Cytisus*, the parasite did not grow vigorously or at high densities on native legumes at the study site.

Field survey

An area of natural vegetation was surveyed to compare the vigour of *Cassytha* on the two target host species and to qualify the condition of infected host plants. In June 2007, 24 2×2 m quadrats were sampled located randomly throughout the study site in the disturbed woodland. Within these areas, data were collected from all shrubs taller than 10 cm (only the data for *Cytisus* and *Leptospermum* are presented here). The height of each shrub and the width of the shrub at the widest point and perpendicular to this were measured to calculate the approximate volume of each shrub. The vigour of each shrub was scored qualitatively as dead, mostly dead, partly alive, or all alive. Mostly dead shrubs had >50% of their stems or leaves dead or discoloured. Partly alive shrubs had some dead or discoloured biomass but this was not >50% of the biomass. *Cassytha* was scored as present on the shrub only when haustorial attachments were observed on the target shrub. *Cassytha* cover was scored visually as low, moderate or high density. Low-density infections covered <10% of the host shrub and *Cassytha* was usually present as a few stems. Moderate density infections covered up to 30% of the host shrub and high density infections covered >30% of the shrub with the *Cassytha* growing in dense coiling mats. The vigour of *Cassytha* on each shrub was scored as dead, vigorous (actively growing, green stems), or low vigour (stems yellowish and no active growth visible).

Cassytha pubescens growth

At the same study site, the growth of *Cassytha* was measured, as stem elongation, on 20 individuals of the two host species selected as described below. The parasite stems were marked by a small paint mark, 30 mm from the stem tip. At least ten *Cassytha* shoots were marked on each host where actively growing stem tips could be located. The

stems were marked in winter (late June 2007) and measured in early spring (September 2007). New actively growing *Cassytha* stems on each host were marked in the same way and growth of newly marked stems remeasured in mid-spring (October 2007) and again in summer (December 2007). It was noted whether stems were coiled around the host or self-coiled (coiled around each other).

Above-ground biomass

The above-ground biomass of 20 uninfected and 20 infected host plants of each species and *Cassytha* on infected plants was harvested. It was ensured that the *Cassytha* on the infected plant was not attached to other hosts and occurred at moderate to high densities. This restricted plant choice and prevented all plants being selected of approximately equal size. Uninfected plants were selected to match the range of sizes of infected plants. The plants were harvested in December 2007 and January 2008. The biomass was oven-dried at 70 °C and separated into stem, leaf and parasite stem components before weighing. *Cytisus* stem biomass was further subdivided into woody stems and photosynthetic stems.

Photosynthesis

Eight *Cytisus* infected by *Cassytha* and eight non-infected plants and six each of *Leptospermum* were selected for physiological measurements. All host plants were mature with moderate to high intensity infections of *Cassytha* and situated in open areas that were unshaded for at least half of the day. Measurements of net assimilation rates and transpiration were made on plants during October 2007 (spring) using a CIRAS-2 infra-red gas analyser (PP Systems, Amesbury, MA, USA). For *Cytisus*, the first fully expanded leaf was measured from the top of the plant on the northern side of the shrub. *Leptospermum* leaves grow in small, erect clusters so measurements were made on the first fully expanded cluster of leaves on the uppermost, northern side of the shrub. For *Cassytha* measurements, two green portions of stem were selected that were located below the young, soft growing tips. Leaf area was determined by tracing leaves on graph paper before insertion into the leaf chamber. A standardized stem area was used for *Cassytha*, as stems are of similar diameter. Measurements were made on well-watered plants (natural rainfall) under saturating irradiance, with photon flux density greater than $1400 \mu\text{mol m}^{-2} \text{s}^{-1}$. Measurements were made between 0830 and 1030 h, on plants that had been in unshaded conditions for at least 30 min.

To determine whether plants infected with *Cassytha* became stressed, photosystem II (PSII) efficiency was measured during the afternoon and recovery assessed after a short period in the dark. PSII efficiency was measured on the same set of plants as above, after plants had been exposed to full sun for at least the previous 4 h. Measurements were made with a Mini-PAM Portable Chlorophyll Fluorometer fitted with a 2030-B leaf-clip holder (Heinz Walz GmbH, Effeltrich, Germany). A single measurement of yield was made between 1400 and 1500 h under ambient light conditions. The leaves or stems were then covered in aluminium foil. After 30 min the foil was removed and yield was remeasured. The measurements

were repeated pre-dawn to determine the maximum quantum yield after an extended recovery period overnight. Plants were sampled at three separate times in October and November 2007.

Statistical analyses

The categorical survey data were analysed using nominal logistic models. For host biomass data, ANCOVA was used to compare photosynthetic tissue allocation between infected and uninfected plants, using woody stem biomass as a covariate. For *Cytisus*, allocation to leaves between infected and uninfected plants was also compared with photosynthetic stem biomass as the covariate. ANCOVA was also used to compare *Cassutha* biomass on the two host species, with total host above-ground biomass as the covariate. Analysis of variance was used to compare transpiration rates and maximum photosynthetic rates between infected and uninfected plants, testing each species separately. Repeated measures ANOVA (MANOVA) was used to compare yield measures for uninfected control plants, host plants infected by *Cassutha* and the parasite. Matched pair *t*-tests were used to assess short-term recovery in each treatment category, testing a one-tailed probability that yield increased after the recovery period. The statistical package JMP Ver. 4.0.3 (SAS Institute Inc., 2000) was used for analyses.

RESULTS

Survey

Cytisus scoparius occurred more frequently within the surveyed plots than *Leptospermum*, due mainly to an abundance of *Cytisus* seedlings. However, the volume of both target host plants per unit area was similar (*Cytisus* volume mean \pm s.e., $0.61 \pm 0.14 \text{ m}^3 \text{ m}^{-2}$, $n = 603$; *Leptospermum*, $0.49 \pm 0.10 \text{ m}^3 \text{ m}^{-2}$, $n = 133$). *Cassutha* occurred in 65% of sampled plots. On a biomass basis, the availability of the two species as hosts for *Cassutha* was similar; however, on an individual plant basis, *Cytisus* was a more available host than *Leptospermum*. *Cassutha* utilized *Leptospermum* as a host at higher proportions than its availability in each plot. *Leptospermum* comprised 13% of the individuals sampled and was host to 22% of the *Cassutha* sampled. Conversely, *Cytisus* comprised 61% of all shrubs sampled and was host to 65% of the parasite sampled. *Cassutha* preferentially infected taller plants of both species [likelihood ratio (LR) $\chi^2 = 91.73$, d.f. = 1, $P < 0.0001$] with a height (mean \pm s.e.) of infected plants of $0.97 \pm 0.03 \text{ m}$ and uninfected plants $0.61 \pm 0.02 \text{ m}$.

There was no significant difference in the density of *Cassutha* on the two host species (LR $\chi^2 = 1.81$, d.f. = 4, $P = 0.40$). Approximately half of the infected plants had infections of *Cassutha* classified as moderate to high intensity (Fig. 1A). *Cassutha* vigour varied with host species (LR $\chi^2 = 66.36$, d.f. = 4, $P < 0.0001$). A high proportion of the *Cassutha* growing on *Cytisus* hosts was vigorous whereas *Leptospermum* had higher proportions of non-vigorous *Cassutha* (Fig. 1B).

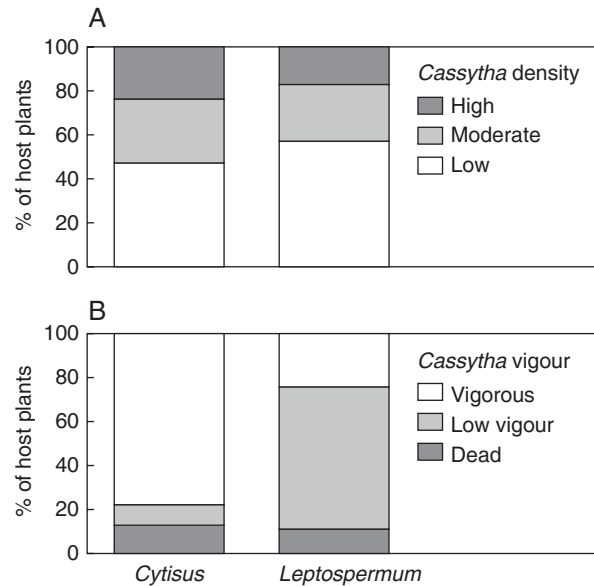


FIG. 1. Frequency histograms of the proportions of *Cassutha pubescens* in different density classes on the two host species *Cytisus scoparius* and *Leptospermum myrsinoides* (A), and the vigour of *Cassutha* on the two host species (B).

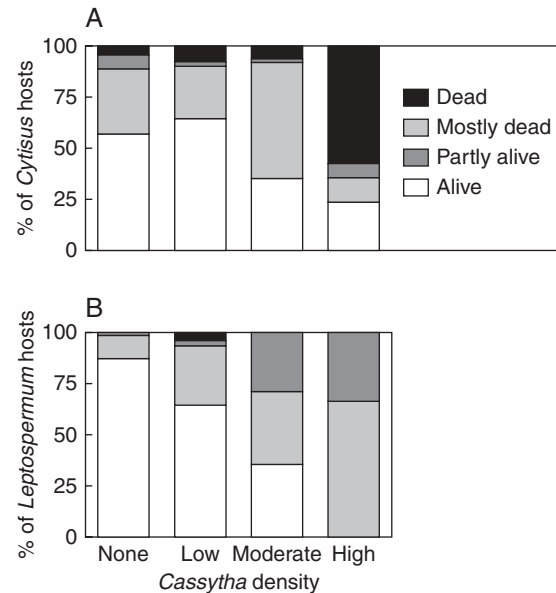


FIG. 2. Frequency histograms of the proportions of *Cytisus scoparius* (A), and *Leptospermum myrsinoides* (B), in different condition classes infected by *Cassutha pubescens* of increasing density.

Host condition varied with the density of *Cassutha* (*Cytisus* LR $\chi^2 = 100.45$, d.f. = 9, $P < 0.0001$; *Leptospermum* LR $\chi^2 = 49.73$, d.f. = 9, $P < 0.0001$). The highest proportion of dead *Cytisus* occurred where *Cassutha* density was high (Fig. 2A). All *Leptospermum* plants with high density infections of *Cassutha* had at least some dead biomass but mortality was not associated with the presence of the parasite (Fig. 2B).

Cassytha growth

Cassytha stem growth rates were significantly higher on *Cytisus* hosts than on *Leptospermum* hosts over the three periods when measurements were made (Fig. 3A). Although *Cassytha* growth rates continued to increase on *Cytisus* hosts across the three measurement periods, on *Leptospermum* hosts growth rate did not increase from October to December (MANOVA time \times species interaction, numerator d.f. = 2, denominator d.f. = 19, exact $F = 27.96$, $P < 0.0001$). New growth of *Cassytha* on *Cytisus* hosts coiled around host stems early in the growing season, whilst new growth of *Cassytha* stems coiled around *Leptospermum* stems later in the season (Fig. 3B). Most of the new growth on *Cytisus* later in the season was self-coiling, with the stems growing upright and self-coiling.

Host and parasite biomass

Leaves comprise a very small proportion of the total biomass of *Cytisus* with most of the photosynthetic biomass occurring in the stems. Infected plants had significantly less photosynthetic biomass than uninfected plants (ANCOVA, $F = 2.27$, d.f. = 1, $P < 0.03$; Fig. 4A). For infected plants, leaves contributed significantly less to the photosynthetic biomass than in uninfected plants (ANCOVA, $F = 19.97$, d.f. = 1, $P < 0.0013$; Fig. 4B). Infected *Leptospermum* had lower leaf biomass than uninfected plants but this difference was not significant (ANCOVA, $F = 3.68$, $P = 0.063$; Fig. 4C).

There was significantly less *Cassytha* biomass on *Leptospermum* than *Cytisus* (ANCOVA, d.f. = 1, $F = 9.537$, $P = 0.004$). The biomass of *Cassytha* increased linearly with *Cytisus* individual biomass but there was no significant linear relationship between *Cassytha* and *Leptospermum*

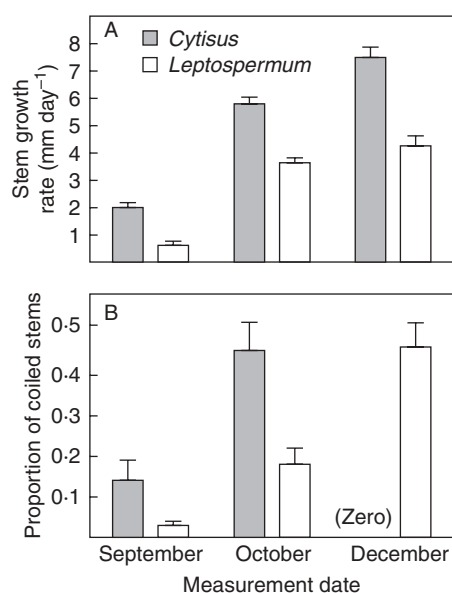


FIG. 3. *Cassytha pubescens* stem growth rate (A) and proportion of stems coiled onto host (B) on *Cytisus scoparius* and *Leptospermum myrsinoides* hosts over three growth periods (means \pm s.e., $n = 20$ for each host species).

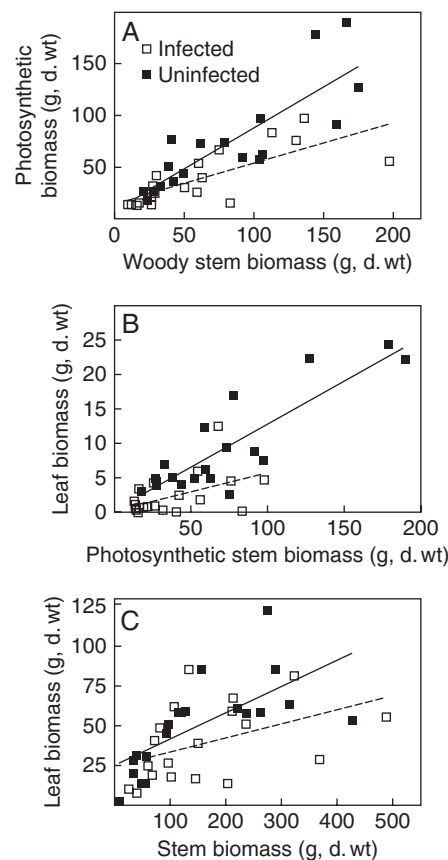


FIG. 4. Biomass of plants infected by *Cassytha pubescens* and uninfected plants showing the relationship between (A) woody stem biomass and photosynthetic biomass of *Cytisus scoparius* ($n = 19$), (B) photosynthetic biomass and leaf biomass of *Cytisus*, and (C) stem biomass and leaf biomass of *Leptospermum myrsinoides* ($n = 20$). Regression lines are shown for illustrative purposes only.

biomass (Fig. 5). *Cassytha* comprised $35 \pm 7\%$ (mean \pm s.e.) of the total above-ground biomass of the *Cytisus* host-parasite association. For many infected *Cytisus* plants, the biomass of the parasite was greater than the photosynthetic biomass (stems and leaves) of the host plant (mean \pm s.e., $104 \pm 31\%$). The proportion of *Cassytha* biomass in relation to *Leptospermum* hosts was lower than that for *Cytisus*, comprising $11 \pm 2\%$ (mean \pm s.e.) of the total above-ground biomass and $73 \pm 23\%$ of the leaf biomass.

Photosynthesis

For both host species, plants infected by the parasite had significantly lower photosynthetic rates than uninfected plants (Table 1 and Fig. 6A). Infected *Cytisus* had significantly lower transpiration rates per unit leaf area than uninfected plants, although this difference was not observed between infected and uninfected *Leptospermum* (Fig. 6B).

Cassytha growing on *Cytisus* had significantly lower photosynthetic rates than either infected or uninfected *Cytisus* (Fig. 6A). In contrast, photosynthetic rates of parasites growing on *Leptospermum* were similar to those of infected plants, but significantly lower than those of uninfected

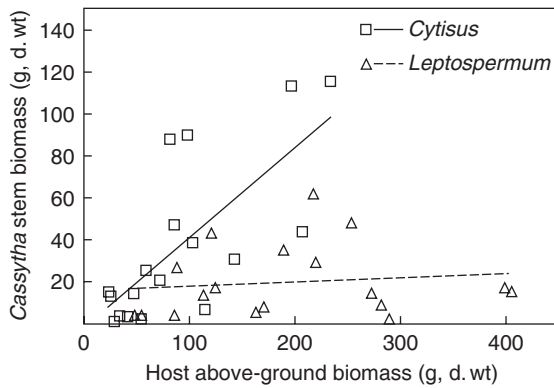


FIG. 5. Relationship between *Cassytha pubescens* biomass and the total above-ground biomass of host plants, *Cytisus scoparius* and *Leptospermum myrsinoides*. Linear regression lines: *Cytisus*, $n = 18$, $F = 17.48$, $P < 0.001$; *Leptospermum*, $n = 18$, $F = 0.22$, $P = 0.65$.

TABLE 1. Results of ANOVA testing for differences in physiological parameters between the parasite *Cassytha pubescens*, host infected by the parasite and uninfected plants

Host species	Parameter	d.f.	F-statistic	P value
<i>Cytisus scoparius</i>	Net assimilation	2	42.20	<0.0001
	Transpiration	2	3.38	0.053
<i>Leptospermum myrsinoides</i>	Net assimilation	2	7.16	0.007
	Transpiration	2	8.17	0.031

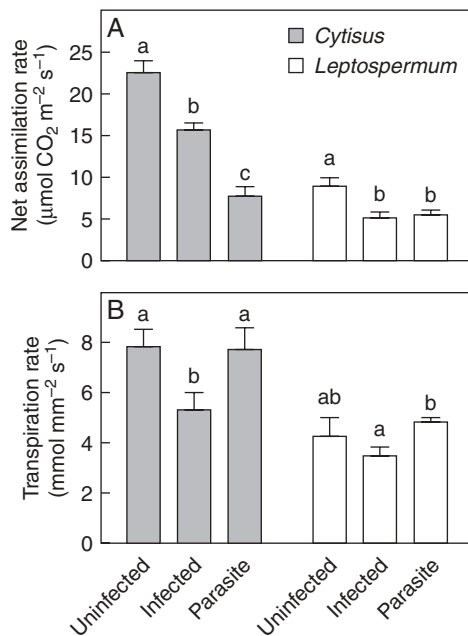


FIG. 6. (A) Net assimilation rates and (B) transpiration rates for *Cytisus scoparius* and *Leptospermum myrsinoides* infected by *Cassytha pubescens*, and uninfected hosts (means + s.e., *Cytisus* $n = 8$; *Leptospermum* $n = 6$). Different letters indicate significant differences between plant treatments (separate Tukey–Kramer pairwise comparisons for each species).

Leptospermum. On both host species, the transpiration rate of *Cassytha* was significantly higher than the infected host (Fig. 6B).

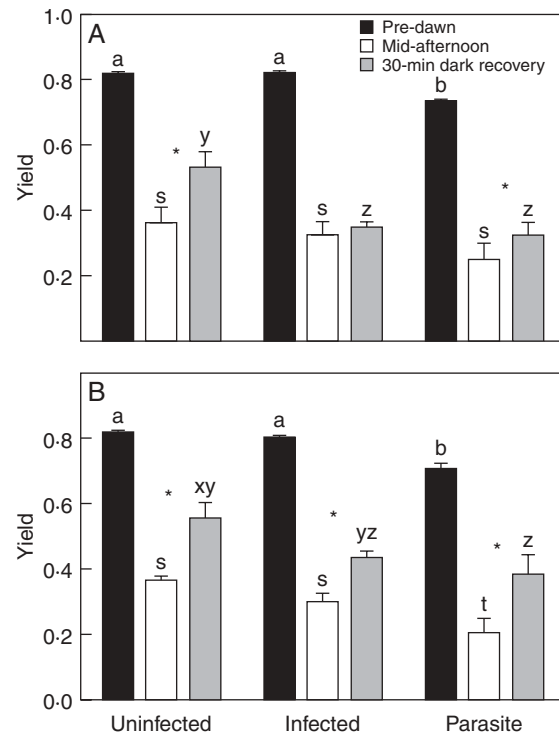


FIG. 7. Pre-dawn yield, mid-afternoon yield and yield after a 30-min dark recovery period in the mid-afternoon for (A) *Cytisus scoparius* and (B) *Leptospermum myrsinoides* plants, infected by *Cassytha pubescens*, uninfected, and the parasite (means + 1 s.e., *Cytisus* $n = 8$; *Leptospermum* $n = 6$). Asterisks indicate significant differences between measurement times (not including pre-dawn measurements; separate Tukey–Kramer pairwise comparisons).

Photosynthetic efficiency

Cassytha had significantly lower pre-dawn yield than either of the host species on which it was growing (Fig. 7A, B). Mid-afternoon yield of *Cassytha* was lower than *Leptospermum* hosts but not *Cytisus* hosts (Fig. 7A, B). Short-term recovery of *Cassytha* PSII efficiency occurred on both host species with measured yield significantly greater after a short recovery period.

There was no difference in the mid-afternoon or pre-dawn yield of *Cytisus* plants that were infected by *Cassytha* and uninfected plants. However, the short-term recovery of *Cytisus* was faster in uninfected plants than in infected plants as infected plants showed no significant increase in yield after a short recovery period (Table 2).

TABLE 2. Results of matched pair *t*-tests of the null hypothesis that yield is not higher after a period of 30 min dark recovery for the parasite *Cassytha pubescens*, two host species infected by the parasite and uninfected controls

Host species	Treatment	d.f.	$P > t$
<i>Cytisus scoparius</i>	Uninfected	7	0.027
	Infected	7	0.283
	Parasite	7	0.031
<i>Leptospermum myrsinoides</i>	Uninfected	5	0.004
	Infected	5	0.03
	Parasite	5	0.008

There was no difference in the mid-afternoon or pre-dawn yield of *Leptospermum* plants that were infected by *Cassytha* and uninfected plants. Both infected and uninfected *Leptospermum* showed some short-term recovery in photosynthetic efficiency with significantly higher yields after a short recovery period (Table 2).

DISCUSSION

The present results show that the native generalist parasite *Cassytha* has a greater effect on the physiology and vigour of a novel host, *Cytisus*, than on a co-occurring, native host, *Leptospermum*. Although the parasite shows a slight preference for the native host it grows to high densities on both host species. However, host susceptibility to infection and the virulence of the parasite was greater on the introduced host than the native host. Although tolerance and resistance to infection may explain the reduced impacts of *Cassytha* on the native host, the higher impacts on the introduced host could also be the result of the higher resources that this host provides. When these resources support improved parasite growth, this can lead to a decline in host performance.

It was found that the assimilation rates of *Cassytha* were similar to its native host *Leptospermum* although lower than the introduced host, *Cytisus*. Parasite assimilation rates recorded during this study were much higher than those previously published for the South African species *Cassytha ciliolata* and *C. filiformis* (De La Harpe *et al.*, 1981) and the morphologically similar genus *Cuscuta* (Stewart and Press, 1990). These authors considered that the autonomous carbon gain of *Cassytha* and *Cuscuta* was barely sufficient to replace respiratory losses. Despite the capacity for *Cassytha* to assimilate carbon, the parasite may still obtain a proportion of carbon from its host, other studies showing that from 28 % to 99 % of hemi-parasite carbon may be host derived (Graves *et al.*, 1989, 1990; Marshall and Ehleringer, 1990).

Cassytha performance, in terms of net assimilation rates, growth rates and accumulated biomass, were poorer on the native host than on the introduced host. The parasite may have greater access to the resources that *Cytisus* provides due to either the higher nutrient status of this species or the reduced resistance to transfer of resources across the haustorium. Experimental manipulations of host nutrient status have demonstrated that holo-parasite performance increases with increases in host nitrogen (Marshall *et al.*, 1994; Jeschke and Hilpert, 1997; Pennings and Simpson, 2008). However, where a parasite and its host have co-evolved, such as is potentially the case of the *Cassytha*–*Leptospermum* association, the development of host resistance mechanisms, particularly those that result in the degeneration or obstruction of haustorial tissue may have greater effects on nutrient transfer and hence parasite performance (Jiang *et al.*, 2008). Chemical defences produced by the host may also have detrimental effects on parasite metabolism, particularly when they interfere with photosynthetic performance (Cameron *et al.*, 2008).

Although both host species were affected by *Cassytha* infection, *Leptospermum* appeared to be less susceptible than *Cytisus*. Transpiration, allocation to leaf biomass and survival were not significantly reduced in infected *Leptospermum* relative to uninfected plants. In addition, infected plants rapidly

recovered PSII efficiency. *Cytisus* was more negatively impacted by *Cassytha*. Photosynthesis, transpiration, allocation to photosynthetic biomass and survival were significantly reduced in infected plants.

Significant decreases in the photosynthesis of infected *Cytisus* and *Leptospermum* were measured. Parasites can reduce host carbon fixation by lowering host stomatal conductance, impacting host photosynthetic metabolism or changing host biomass, biomass allocation or architecture (Graves, 1995; Press *et al.*, 1999; Watling and Press, 2001). The present results suggest there could be some stomatal limitation to photosynthesis as infected plants had lower transpiration rates than uninfected plants. However, other direct impacts of the parasite on photosynthetic metabolism through reductions in carboxylation efficiency and thylakoid capacity (e.g. Watling and Press, 2000; Cameron *et al.*, 2008) require further examination. The slower rates of recovery of PSII efficiency in infected *Cytisus* indicate irradiance stress. The reduced photosynthetic rate in infected plants can increase the likelihood of photoinhibition (Watling and Press, 2001) but there were no long-term photoinhibitory effects as PSII efficiency recovered overnight. In addition, changes in the proportion of photosynthetic biomass, particularly in *Cytisus*, could have large impacts at the whole plant level. Heavy infestations can also create a shading effect, reducing the light available for photosynthesis. This ‘strangling’ effect has been observed in the parasite *Cuscuta* (Jeschke and Hilpert, 1997), which has a similar growth habit to *Cassytha*.

Suppression of photosynthesis can result in lower growth rates and biomass accumulation by the host but resource extraction by the parasite may also have the same effects. As parasite biomass increases in relation to host biomass, resource extraction may become more important (Graves *et al.*, 1989). For *Cytisus*, parasite biomass frequently exceeded host photosynthetic biomass, therefore resource extraction in heavily infected plants could significantly increase mortality rates. Although *Cassytha* reached high densities on both host species, the present results suggest these infections develop at different rates. *Cassytha* stems coiled around *Cytisus* early in the growing season and around *Leptospermum* late in the growing season. The extraction of resources from *Cytisus* therefore commences earlier enabling the parasite to grow beyond the host plant, resulting in high parasite loads relative to host biomass. Conversely parasitic biomass on *Leptospermum* was typically confined to the host plant stems. Slow growth rates of *Cassytha* on *Leptospermum* may enable the host species to persist, with the high intensity infections developing over several years. High intensity infections of *Cassytha* were associated with mortality of *Cytisus* but not *Leptospermum*. In this dynamic process, *Cassytha* growth on *Cytisus* is rapid and the survey results show that these high parasite densities are correlated with host mortality.

Conclusions

Significant differences were found in the impacts of a parasitic plant on the growth and physiology of two host species under field conditions. There is evidence that declines in host condition may be the result of suppression of photosynthesis by the parasite but resource extraction by the parasite

could also have significant impacts. In addition, the less affected native host, *Leptospermum*, may have evolved some resistance mechanisms to *Cassytha* infection. These mechanisms can operate at different stages of the infection process and result in degeneration or obstruction of the haustoria, chemical and physical barriers to haustorial penetration and/or abortion of parasitic tissues (Bringmann *et al.*, 1999; Bouwmeester *et al.*, 2003; Cameron *et al.*, 2006; Rispaill *et al.*, 2007; Rümer *et al.*, 2007).

The ERH predicts that invasive species will thrive in invaded communities when they are released from the controlling effects of their native enemies. *Cytisus* has encountered a new parasite, *Cassytha*, in its invaded range which has stronger impacts on this species than another co-occurring native species. However, *Cytisus* continues to spread in native vegetation which suggests that other factors favour its performance. The acquired native enemy, *Cassytha* may not be abundant enough to resist initial invasion by *Cytisus*. In this system biotic resistance is unlikely to prevent invasions, but this process may be an effective regulator of populations of invading species (Levine *et al.*, 2004). It may be feasible for introduced species to be maintained at population levels where they have reduced detrimental effects on the invaded community. A native enemy, such as the parasitic plant *Cassytha* could be an effective natural biocontrol agent for *Cytisus*, with the advantage of having no lethal impact on native species. Further research is required to examine the interaction between the parasite and native and introduced hosts to evaluate the potential for introduction of the parasite into native vegetation invaded by *Cytisus*.

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