Biol Invasions (2025) 27:224
https://doi.org/10.1007/s10530-025-03681-7

ORIGINAL PAPER

The demise of enemy release associated with the recruitment of natural enemies on an invasive tree

Grant D. Martin · Stephanie L. Payne · Sandy-Lynn Steenhuisen · Tapiwanashe Mashamba

Received: 4 July 2025 / Accepted: 19 September 2025 / Published online: 4 October 2025

Abstract *Salix* species, commonly called Willows, are a diverse group originating from Northern Temperate regions but invasive in many parts of the world, including South Africa's Grassland Biome. Willows impact biodiversity, disrupt ecosystems, and cause economic losses. The two most prominent invasive willows there are *Salix babylonica* (weeping willow) and *Salix*×*fragilis* (crack willow). Both were historically reported as the most widespread and damaging invasive tree species in the biome. We reassessed *S. babylonica's* population size and demographics comparing historical aerial photographs to recent satellite images and through targeted roadside surveys. Additionally, we surveyed associated insect herbivores and plant pathogens. Results showed limited recruitment of *S. babylonica*, including a significant decline in adult tree numbers. Population demographics from roadside surveys suggest an aging population primarily of mature or dying trees. Surveys of associated insect herbivores and plant pathogens documented 16 insect families (including three non-native insects), a polyphagous crown gall bacterium and one rust fungus. We suggest these associated enemies contribute to the reduced vigour of *S. babylonica*, offering relief to landowners and conservation authorities that populations are declining. Limited resources can potentially be redirected to managing other more aggressively invading woody species in the Grassland Biome.

Keywords Biological control · Grassland Biome · Invasive alien plants · Willows

G. D. Martin (✉) · S. L. Payne · S.-L. Steenhuisen · T. Mashamba
Afromontane Research Unit, Department of Plant Sciences, University of the Free State, Qwaqwa Campus, Phuthaditjhaba 9866, South Africa
e-mail: g.martin@ru.ac.za

G. D. Martin
Centre for Biological Control, Department of Entomology and Zoology, Rhodes University, Makhanda 6140, South Africa

Introduction

Invasive alien plants are a leading driver of global biodiversity loss, and South Africa is particularly affected, with hundreds of non-native plant species established across all biomes. Notably, the country has experienced more invasive tree introductions than any other region worldwide (Moran et al. 2011). Of the 759 naturalized plant species in South Africa, 240 are trees, with 200 classified as invasive. Among the most impacted biomes is the Grassland Biome, where dominant invasive tree genera include *Acacia*, *Casuarina*, *Eucalyptus*, *Pinus*, *Prosopis*, and *Salix* (Kotzé et al. 2025). Two particularly problematic *Salix* species are *Salix babylonica* L. (weeping willow) and *Salix*×*fragilis* L. (crack willow), both of which are highly invasive in South Africa, especially in grassland regions (Henderson 2020). *Salix babylonica* was introduced by European settlers for ornamental purposes and riverbank stabilization, while *S.×fragilis* was later imported by the government in an attempt to establish a basket-weaving industry (Immelman 1973; Henderson 2020).

Extensive surveys in the 1970s and 1980s in South Africa's Grassland Biome showed *S. babylonica* to be the most widespread riverine invader in the biome, forming continuous—sometimes kilometres-long—pure stands along perennial watercourses (Henderson 1991). In addition to historical plantings at dams and riverbanks, its spread was primarily due to self-propagation (vegetative) and floodwater dispersal, posing a threat to indigenous riparian species and potentially altering hydrology, while *S.×fragilis* was less common but still noticeable (Henderson 1991). Within South Africa, The Conservation of Agricultural Resources Act (CARA) of 1983 lists both species as Category 2 invaders, recognizing their potential for spread but also acknowledging certain advantageous traits that make them worth keeping under specific conditions (CARA 1983).

When a plant is introduced outside of its native distribution, it typically leaves behind its natural enemies, such as herbivorous insects and fungal pathogens, a phenomenon known as the Enemy Release Hypothesis (ERH) (Keane and Crawley 2002). The ERH predicts that this escape from natural enemies gives introduced plants a competitive advantage over native plants in the introduced range (Crawley 1997). Based on three key assumptions, the ERH suggests that natural enemies regulate native plant abundance, have greater impact on native than invasive species, and benefit invasive plants by reducing regulator natural enemies (Keane and Crawley 2002). This advantage may be diminished through the introduction of natural enemies associated with the plant. Such introductions can occur in many ways, but three primary mechanisms are most notable. First, classical biological control, founded within the ERH, which involves deliberately reuniting invasive species with their co-evolved, host-specific natural enemies from the native range and is used by many countries as a management tool (McFadyen 1998). This method relies on rigorous screening to ensure specificity and minimize non-target effects. Second, accidental biological control operates similarly but arises from unintentional introductions, such as through global trade or travel, where natural enemies stow away or are introduced without formal assessment (Medzihorský et al. 2024). Third, phylogenetic host jumps can occur when invasive plants are closely related to native species. Insect herbivore preference is strongly influenced by plant phylogeny, with most insects restricted to feeding on closely related plants (Forister et al. 2015; Gougherty and Davies 2021). As a result, natural enemies of native plants may expand their range to attack invasive relatives (Wingfield et al. 2015; Crous et al. 2016). Such shifts are more likely when non-native plants are closely related to regional native species, increasing the chance of native insects adopting them as novel hosts (Branco et al. 2015). In the case of willows, this may be important as South Africa has a native willow species, *Salix mucronata* Thunb., which occurs in the same environments as the two introduced species (Immelman 1987).

The longer a species spends outside its native range the higher the likelihood of recruiting natural enemies, both native as well as introduced. An example illustrating this concept is *Robinia pseudoacacia* L. (black locust), a sparsely populated tree species in its limited native range in the eastern USA. In contrast, it has become highly invasive, especially in disturbed environments, in most temperate world regions. In Europe, the plant was introduced in the 1600 s, where it rapidly spread to become the most widespread terrestrial tree across Europe (Martin 2019; Medzihorský et al. 2024). Since its initial introduction, several associated herbivores, including a galling midge (*Obolodiplosis robiniae* Haldeman, Diptera: Cecidomyiidae), two leaf-mining microlepidopterans (*Phyllonorycter robiniella* Clem. and *Parectopa robiniella* Clem., both Lepidoptera: Gracillariidae), a sawfly (*Nematus tibialis* Newman, Hymenoptera: Tenthredinidae), and an aphid (*Aphis robiniae,* Hemiptera: Aphididae), have established in Europe from the USA, significantly impacting the tree (Sheppard et al. 2006; Duso and Skuhravá 2002; Medzihorský et al. 2024). Therefore, certain scenarios may lead to associated insects re-uniting unaided or by accident and having a controlling impact (Strong et al. 1977; Crous et al. 2016).

The likelihood of attack may also be associated with plant abundance. When a non-native plant becomes widespread in a region, either through its invasiveness or because of being extensively planted for agricultural, horticultural, or forestry purposes, it is more likely to accumulate native insects as well as its own associated species (Wingfield et al. 2015; Crous et al. 2016). This is a common occurrence globally, especially among widely planted forestry species which have extensive populations (Liebhold et al. 2017). Within these examples, especially forestry species, this often results in a decrease in species vigour (Hurley et al. 2016; Brockerhoff and Liebhold 2017).

Therefore, in general, introduced species slowly accumulate enemies over time (Hurley et al. 2016; Brockerhoff and Liebhold 2017; Medzihorský et al. 2024). When a species is regarded as beneficial or having beneficial attributes, this accumulation of additional specialist herbivores through invasions may ultimately lead to a decrease in the benefits provided by non-native plants (Gutierrez and Ponti 2013). While in the case of species regarded as damaging rather than beneficial, this may lead to a reduction in impacts and perceived threats; however, these relationships are infrequently documented when outside of a biological control system or in tree systems due to the longer time frames required to note population level changes. The spread of *S. babylonica* in South Africa provides an interesting case study where a non-commercial tree has accumulated several insect pests diminishing its invasive potential, leading to reduced vigour, as recent observations suggest that *S. babylonica* may have become less invasive and therefore have decreased impacts, with limited recruitment observed in South Africa. Here we hypothesize that *S. babylonica* is experiencing a diminishing enemy release with the accumulation of associated enemies, potentially explaining a population-level crash that aligns with the ‘now you see them, now you don’t phenomenon observed in other established invaders (Simberloff and Gibbons, 2004).

Methods

The study focused on assessing population size changes of *S. babylonica* in the Grassland Biome of South Africa (Fig. 1). The Grassland Biome is characterized by its diverse vegetation, dominated by

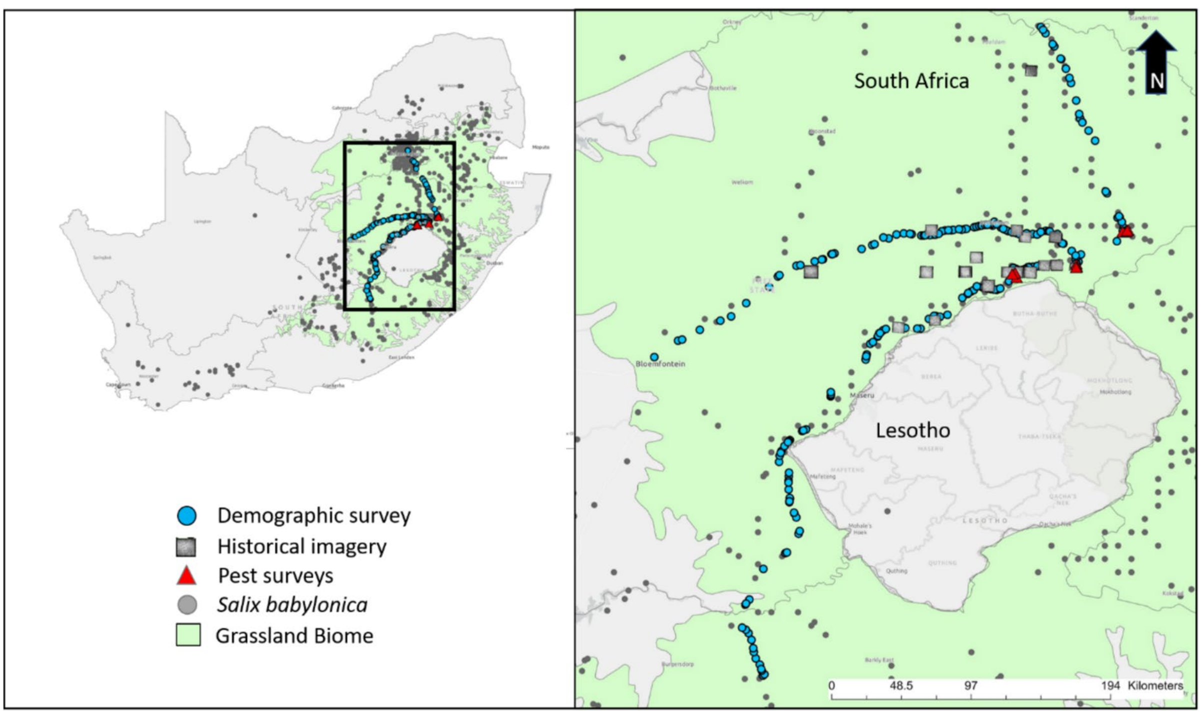

Fig. 1 Map of South Africa showing the Grassland Biome (light green), locations of *Salix babylonica* demographic surveys (blue circles), regions selected for historical imagery analysis (grey squares), and the location where a pest associated with *S. babylonica* were sampled (red triangles)

shrubs and grasses, with Poaceae, Asteraceae, and Fabaceae families being the most prominent (Mucina and Rutherford 2006). Tree species found within the biome are mostly all invasive except for some native species such as *Leucosidea sericea* Eckl. & Zeyh. (Rosaceae) and the native *Salix* species *S. mucronata* (Davy 1922; Gwate et al. 2024). The biome has experienced significant habitat changes over the past decades from woody species densification (Skowno et al. 2017), overgrazing, changing fire regimes and land use transformation (SANBI 2013; Martin 2021).

Assessing population decline in Salix species using historical and contemporary aerial imagery

To confirm suspected decreasing population sizes, historical imagery was obtained from the Cartographic Design and National Geospatial Infrastructure (CDNGI) Digital Portal. Within this digital portal, an active map with areas in the Free State and Gauteng provinces invaded by *S. babylonica* populations was selected (Cartographic Design and National Geospatial Infrastructure (https://ngi.dalrrd.gov.za/). The primary objective was to locate suitable imagery from 1984 which were at a 1: 30,000 scale, resulting in an area of ~ 5 km^2 per photograph (Fig. 1). When potential images were identified, further checks were conducted to ensure that the images were captured during months when willows had foliage present and the image quality was sufficient, with minimal cloud cover to facilitate accurate species identification. Thirteen usable images were acquired through this method. These images were georeferenced to satellite imagery using the World Geodetic System 1984 (WGS84) as the coordinate reference system. All georeferencing and subsequent analysis were performed using geoprocessing tools in ArcMap version 10.7.1. After georeferencing, point locations were manually digitized by visually identifying the centre of individual *S. babylonica* trees (Fig. 2). Each point represented coordinates of each tree allowing for a count of each tree identified on the photographs. The coordinates were used for field validation, and the count was used to find the total number of trees on each site. Due to blurring near the edge of images potential trees at the edges were not included. Point locations digitized from the 1984 aerial photographs were superimposed onto the 2023 aerial images, within the ArcGIS platform. This step allowed for direct visual and spatial comparison between the total of the points counted in 1984 and the points counted in 2023 between the two time periods for *S. babylonica* (Fig. 2). To validate the findings, field validation was performed.

The number of trees per site (population size) of *S. babylonica* in 1984 and 2023 were tested for normality using a Shapiro-Wilks test. *Salix babylonica* population sizes were not normally distributed ($P = 0.04$) and were log-transformed, which resulted in them becoming normally distributed ($P = 0.11$). All variances were equal (Fisher's Ratio test, $P > 0.05$). Number of trees per population in 1984 and 2023 for *S. babylonica* (log-transformed data) were compared with a paired t-test with equal variances. Analyses were conducted in R (Version 4.3.1; R Core Team 2023). Data are presented as mean ± standard error.

Assessing population demographics and sex ratios of Salix species through roadside surveys in the Grassland Biome

To determine the population demographics of *S. babylonica* trees, road surveys were performed (Fig. 1). Roadsides were defined as strips of public or private land on either side of the roads but were limited to 100 m perpendicular to the road. Road surveys were performed between July 2022 and January 2023 by three observers. A total of six routes were taken along the main roads within the Grassland Biome. Each route was selected according to the following criteria: (a) not have been travelled before during the road side survey; (b) be a main national or regional road within the Grassland Biome; and (c) be able to be driven in both directions so that the observer could safely assess populations on both sides of the road unobscured by the road's width (methods derived from Deus et al. 2016). For each population, tree abundance was estimated using a scale (1–5; 6–20; > 20 trees), and the age of trees closest to the observer were estimated based on predefined criteria (Table 1). A total of 366 roadside sites were assessed along ca. 1694 km. Site locations were recorded using a GPS application (Find My GPS Coordinates, Youngmin Koo, version 2.0.63, developed in 2012).

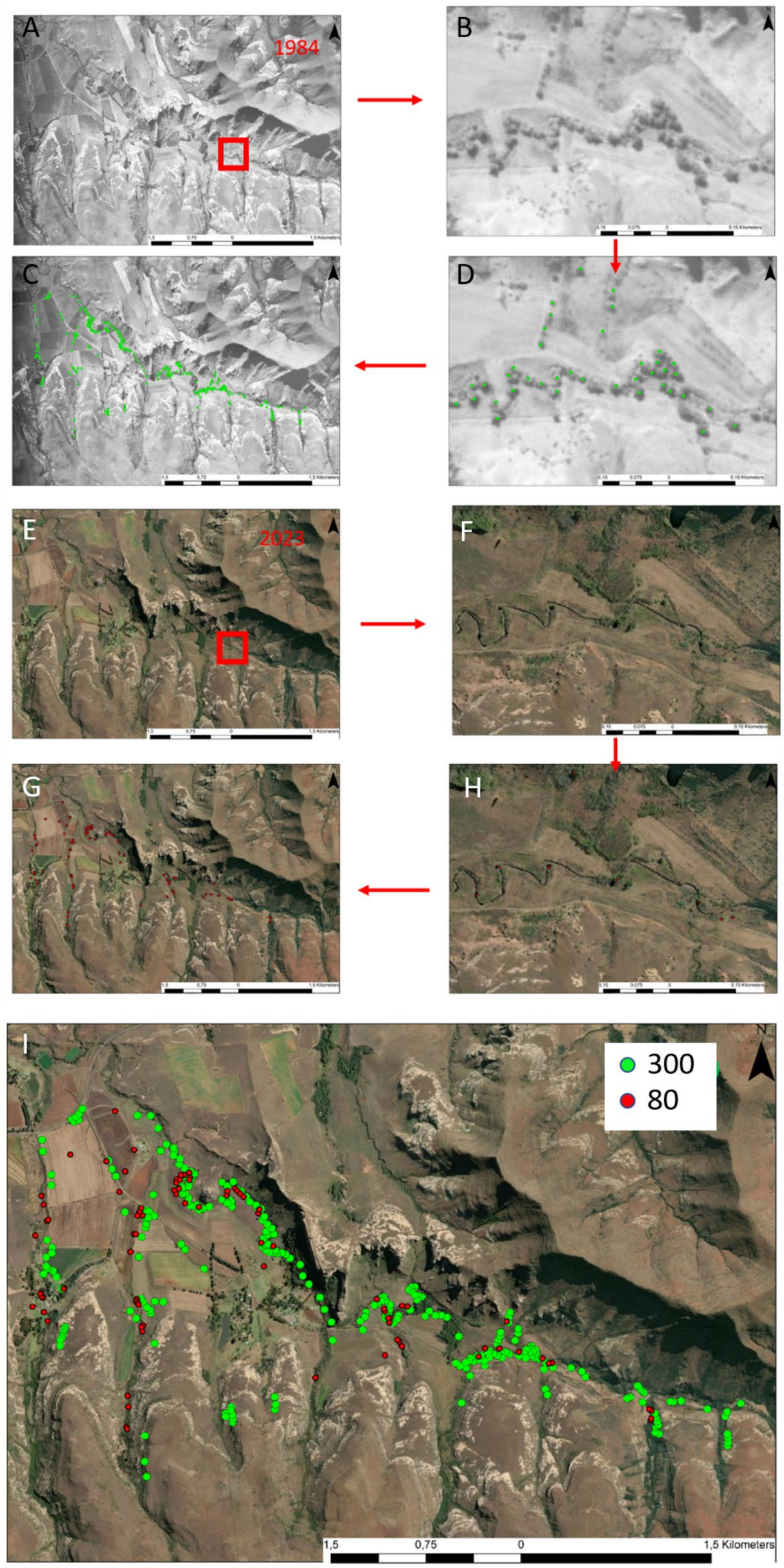

Fig. 2 Location of *Salix babylonica* trees in a study area (28°31′41.42″S, 28°30′47.72″E) in the eastern Free State Grassland Biome, South Africa. **A**–**H** Process of mapping tree locations: green points (historical; 1984 imagery) and red points (current; 2023 imagery). **I** Final composite map showing a reduction in tree occurrences over time (historical in green, current in red)

Table 1 Scale used to assess the age of the *Salix babylonica* trees during roadside surveys

Tree age	Description
1	Seedling < 2 m
2	Young tree > 2 m; < 30 cm at breast height
3	Mature tree (healthy with no broken branches, trunk intact)
4	Mature tree (one or two broken branches, trunk intact)
5	Mature tree (many broken branches, trunk intact)
6	Mature tree (many broken branches, trunk broken)
7	Mature tree (only broken trunk remains, one or two shoots remain)
8	Mature tree (completely dead or rotting trunk remains)

In addition, the combined number of records of *S. babylonica* in South Africa from the South African Plant Invaders Atlas (SAPIA) and GBIF (2024) was plotted

Associated insects

Thirteen randomly located sites, within the study area (Fig. 1) based on access and opportunity, were selected during the road survey. These sites were located between the towns of Harrismith and Clarens in the Grassland Biome. At each site associated pests of *S. babylonica* were sampled. To achieve this, one to four mature trees were sampled once at each site between 08h00 and 14h00 over 4 days (December 2023 and January 2024), resulting in a total of 40 trees sampled. Invertebrates on the foliage of willow trees were collected using a sweep net (40 cm diameter collapsible net) by placing the net over low-hanging branches and vigorously shaking the net in figure-eight motions for 10–15 s per branch. This was repeated 5 times per tree, using different branches for each replicate sample of a tree. All sites where trees were sampled were riparian in nature with some of the sites located on roadsides. All collected invertebrates were transferred to screw-top containers filled with 70% ethanol. Insect and arachnid samples were sorted into families and morphospecies using guidebooks and expertise in the Department of Entomology and Zoology (University of the Free State). The most frequently sampled insects (high abundance or multiple collections) were sent to the National Collections of Insects—Agricultural Research Council—Plant Protection Research Institute (ARC-PPRI) Biosystematics section for full species identifications. Photographs were taken of all diseased tissue and the percentage of each was noted. Where appropriate, photographs were sent to plant pathologists for morphological identification of leaf and stem damage from pathogens (i.e. rusts and fungi).

Species accumulation curves for invertebrates collected for *S. babylonica* were generated over sites, and analysed using regression analysis, to assess sampling effort. All graphs and regression analyses were performed using Microsoft Excel. In addition, available literature and experts were consulted to determine if any insects were omitted, when insects were first recorded, as well as any other valuable information which may have been available on previously observed willow pests.

Results

Population decline in Salix babylonica

The comparison of historical and contemporary aerial imagery showed that the mean density of *S. babylonica* per significantly declined from 82 trees per km^2 in 1984 to 51 trees per km^2 in 2024 ($t_{12} = 3.46$, $P = 0.005$; Fig. 3A). Roadside surveys showed that most *S. babylonica* stands consisted of scattered individual trees along roadways, rivers and streams, with approximately 50% of surveyed sites containing only 1–5 trees (Fig. 3B). Recruitment was extremely limited, as 78% of trees were classified as mature or senescent (Age 5–8; exhibiting signs of decline such as broken main branches), and 99.3% of all surveyed trees were mature (Age 3–8) (Fig. 3B).

Associated insects

Approximately 160 insects, representing 16 families, were collected from the foliage of *S. babylonica* trees sampled in the Grassland Biome (Fig. 4: Appendix 1). The species accumulation curves indicated that sufficient sites had been sampled for *S. babylonica* (Fig. 4 inset). Herbivorous insects constituted 66% of the collected species (Fig. 4). The most frequently

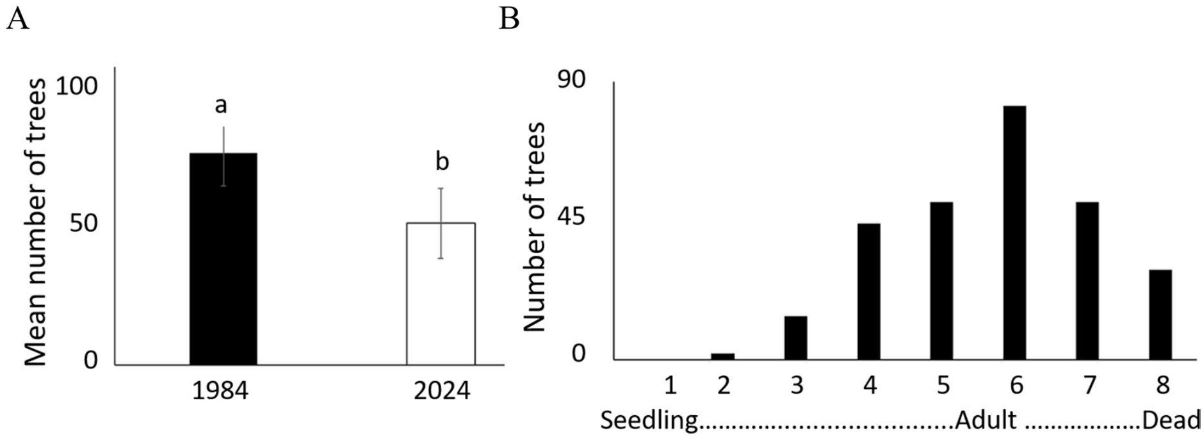

Fig. 3 **A** Number of *Salix babylonica* trees (mean ± standard error) in 1984 and 2024 per site (n = 13 sites) using aerial photographs in the Eastern Free State province, South Africa. Different letters above bars denote a significant difference ($P < 0.05$). **B** Number of trees for each age class of *S. babylonica* recorded during a road survey along main roads within the Grassland Biome

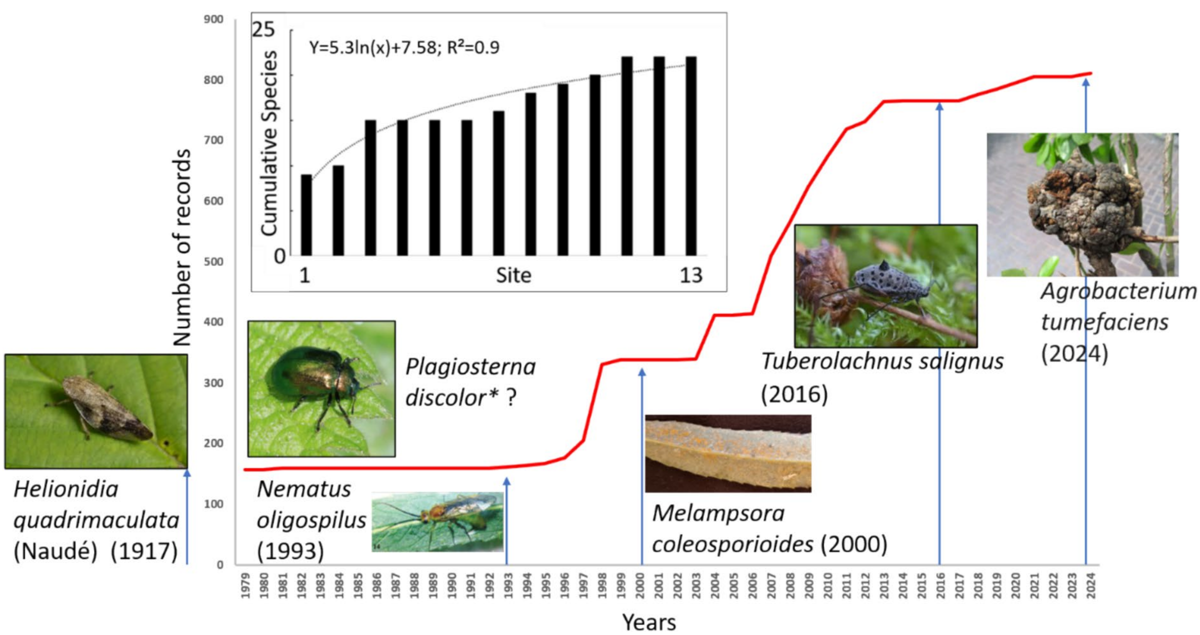

Fig. 4 Cumulative increase (red line) in the number of recorded sites (from herbarium records) for *Salix babylonica* in South Africa (GBIF 2024) and the Southern African Plant Invaders Atlas (Henderson 2007) from 1979–2024. Images show the most abundant recorded non-native pest species and their first recorded date from *Salix* species in South Africa. *Represents the only native species, records of this insect from *Salix* are available from the 1980's. Inset graph: cumulative number of species of invertebrates interacting with *S. babylonica* trees over thirteen sites in the Free State Province, South Africa, analysed using regression analysis. Photo credit: *Helionidia quadrimaculata*—Nikolai Vladimirov, retrieved from Inaturalist.com; *Nematus oligospilus*—Malagon-Aldana et al. (2017); *Tuberolachnus salignus*—Wikipedia.com

collected species included the native willow beetle *Plagiosterna discolor* (Stål) (subfamily Chrysomelinae), the giant willow aphid *Tuberolachnus salignus* (Gmelin) (subfamily Lachninae), the leafhopper *Helionidia quadrimaculata* (Naudé) (subfamily Typhlocybinae), and larvae of the sawfly *Nematus oligospilus* (Förster) (subfamily Tenthredinidae).

In addition, all sampled trees were infected with the willow leaf rust, *Melampsora coleosporioides* as well as the bacterial species, *Agrobacterium tumefaciens* (Fig. 5).

Discussion

Centuries ago, the indigenous *S. mucronata* lined the streams of South Africa's Grassland Biome. However, as European settlers established farms around 200 years ago, they introduced the first plantings of *S. babylonica* (Davy 1922). A century later, the South African government promoted the planting of *S.×fragilis*, in an attempt to establish a basket-weaving industry. By the 1970's, these two exotic species became the most significant riverine invaders in the Grassland Biome, gradually displacing their native counterpart causing significant impacts but also becoming iconic parts of the biome (Henderson 1991). Now, however, our findings reveal a decline in *S. babylonica* populations, and an ageing population with no recruitment which may eventually lead to its complete disappearance from the biome. This reversal aligns with a recognized ecological pattern wherein established invaders unexpectedly crash, a phenomenon that is difficult to document and explain

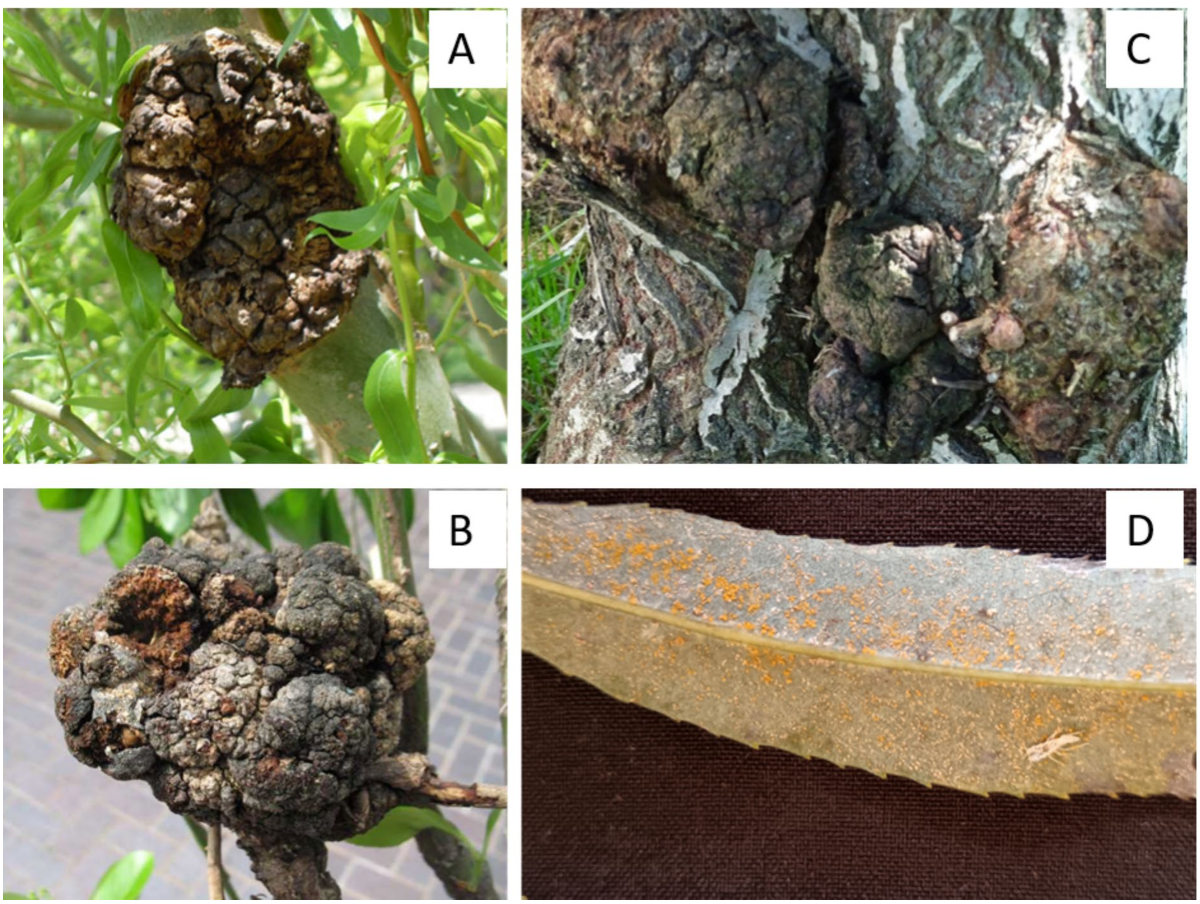

Fig. 5 *Agrobacterium tumefaciens* galls observed on **A** branches, **B** branchlets, **C** trunk, and **D** Rust fungus *Melampsora coleosporioides* on leaves of *Salix babylonica*

mechanistically (See Simberloff and Gibbons, 2004). All living organisms, including trees, are shaped by interacting abiotic and biotic stressors that determine their survival or decline. Isolating the specific drivers particularly at population is a particularly difficult challenge (Teshome 2020). These stressors operate across divergent temporal and spatial scales: some are acute (e.g., pest outbreaks), while others are chronic (e.g., climate change), often compounding in unexpected ways. Trees are no exception, however due to their longer lifespans showing or recording change is more difficult. For example, Impson et al. (2024) took twenty years of data to demonstrate how the introduction of seed-impacting biological control agents, combined with fire, has led to population declines in an invasive Australian *Acacia* species in the fynbos biome.

The persistence or decline of tree populations depends not only on the nature of these stressors but also on their sequence, intensity, and duration. Abiotic drivers such as drought, temperature extremes, and hydrological changes can weaken trees, while biotic agents like insects, pathogens, and competitive species may deliver the final blow or exploit preexisting vulnerabilities (Teshome 2020). Notably, tree mortality is rarely instantaneous; rather, it is often a gradual process shaped by cumulative stress. Among the most pervasive threats are invasive insects, fungal pathogens, prolonged drought, and shifting climate regimes, all of which can interact unpredictably across landscapes (Wood and Morris 2007; Impson et al. 2021; Vacek et al. 2023) and may be playing their part in this example.

Natural enemies are often key stressors which may influence populations. Biological control offers a clear opportunity to measure this relationship. For example, South Africa has released 49 biological control agents (43 insects, 6 fungi) on 20 tree species of which 25 are regarded to have affected their target species at a population level (calculated from Zachariades 2021). In some cases, it may be a single insect but often more than one agent is required to bring a species under control. Here, we documented 16 insect families (including three non-native species), a polyphagous crown gall bacterium, and one rust fungus that have accumulated on *S. babylonica* in South Africa since its introduction. All these organisms likely have some level of impact on the host plant, though determining the exact order of their arrival is challenging. The first species recorded in the literature was *H. quadrimaculata*, collected from *S. babylonica* near Cedara, KwaZulu-Natal Province in 1917 (Theron 1977). Typhlocybinae leafhoppers, such as *H. quadrimaculata*, possess short mouthparts and feed on the palisade cells of plants. Their feeding can cause direct damage to the host, potentially facilitating secondary pathogen infections (Theron 1977; Dworakowska 1992).

The second species recorded on *S. babylonica* was *P. discolor,* a native insect associated with *S. mucronata*. Both larvae and adults of *P. discolor* feed on the foliage of various willow species (Sprecher-Uebersax and Daccordi 2016). Since its indigenous host plant is *S. mucronata* Thunb. subsp. *mucronata*, it is likely that this beetle was among the first to shift onto alien willows once they became established in shared ecosystems. The next recorded insect was *N. oligospilus*, a sawfly native to Europe (De Tillesse et al. 2017; Caron et al. 2011). It was first documented on *S. babylonica* in the Highveld Region of South Africa and the Lesotho Highlands between 1993 and 1994 (Urban and Eardley 1995). The sawfly primarily affects *Salix* species, including *S. babylonica* and *S.×fragilis* (Urban and Eardley 1995; Malagon-Aldana et al. 2017), with minimal impact on native *S. mucronata* (Urban and Eardley 1995). In South Africa, it causes severe defoliation of alien willows (Urban and Eardley 1995), which can stunt growth, impair regrowth, and even lead to tree mortality after repeated infestations (Helbig et al. 2021). The final insect recorded was *T. salignus*, the giant willow aphid, in 2016 (Barkat et al. 2021). Aphids like *T. salignus* cause damage by extracting sap, leading to leaf curling, reduced growth, and honeydew secretion that promotes sooty mould growth, further impairing photosynthesis.

Following these insect records, the rust fungus *M. coleosporioides* was documented in 2000 (Toome and Aime 2015). Rust fungi typically cause leaf discoloration, premature defoliation, and reduced vigour, which may weaken trees over time and increase susceptibility to other stressors (Toome and Aime 2015). Finally, in 2024, crown galls caused by the bacterium *A. tumefaciens* were observed. Crown gall infections disrupt vascular tissues, leading to stunted growth, reduced nutrient transport, and, in severe cases, plant death (Klein and Link 1955). Crown gall disease has been observed in New Zealand affecting populations of poplars and willows (Spiers 1980). It is important to emphasize that all non-native insects and pathogens reported here were accidentally introduced. Their collective impact thus constitutes a case of 'accidental biocontrol', a phenomenon distinct from the planned, targeted releases of classical biological control.

Associated insects are undoubtedly contributing to the decline of the alien *S. babylonica* in South Africa. This decline must also be understood within the context of the species ecology. As pioneer species, willows are light-demanding, poorly competitive as juveniles, and require large-scale disturbances (e.g., floods creating bare sandbars) for successful regeneration (Karrenberg et al. 2002; Van Splunder et al. 1995). In their native ranges, willows like *Salix alba* L. exhibit episodic recruitment linked to such events (Karrenberg et al. 2002) as such recruitment is naturally low. In South Africa, one of the species' primary regenerative strategies is critically compromised as only female plants were recorded which effectively prevents sexual reproduction and seed-based recruitment under current conditions. Consequently, the only remaining mechanism for reproduction (vegetative propagation) is being suppressed by the associated pests outlined above. Other abiotic factors, such as climate change, may also play a role, though these were beyond the scope of this study. Nevertheless, the observed reduction in *S. babylonica* populations provides some relief for landowners and conservation managers, as it may allow limited resources to be redirected toward other invasive or high-priority species within the biome.

Acknowledgements The authors would like to thank the Natural Resources Management Programme of the Department of Environmental Affairs, South Africa and the South African Research Chairs Initiative of the Department of Science and Technology and the National Research Foundation of South Africa. S.S. thanks the University of the Free State's Department of Research and Development's support for rated researchers, for financial support for this project. The authors are also grateful to the three anonymous reviewers and the Associate Editor of Biological Invasions for improving the quality of this article.

Author contributions Grant D Martin: Conceptualization, Methodology, Field work, Writing–review and editing Stephanie L. Payne, Sandy-Lynn Steenhuisen: Writing–original draft, Writing–review and editing, Data curation, Formal analysis. Tapiwanashe Mashamba: Methodology, Field work, Writing–review and editing.

Funding Open access funding provided by Rhodes University. Open access funding provided by Rhodes University. Funding for this work was provided by the Natural Resources Management Programme of the Department of Environmental Affairs, South Africa and the South African Research Chairs Initiative of the Department of Science and Technology and the National Research Foundation of South Africa. Any opinion, finding, conclusion or recommendation expressed in this material is that of the authors and the NRF does not accept any liability in this regard.

Declarations

Conflict of interest The authors have not disclosed any conflict of interests.

Appendix 1

See Table 2.

Table 2 List of insects and arachnids found on *Salix babylonica* trees over 13 sites in the eastern Free State, South Africa. Insects are organised in their orders and families, but those that were not identified to species level are labelled as morphospecies

Salix babylonica				
Order	Invertebrate family/species	Insects per tree (mean ± SE)	Infested trees (%, N = 40)	Total number of invertebrate individuals
	Insecta			
Coleoptera	Chrysomelidae			
	Plagiosterna discolor	2.5 ± 0.5	30	30
	Chrysomelidae sp 1	1	2.5	1
	Chrysomelidae sp 2	1	2.5	1
	Chrysomelidae sp 3	1	2.5	1
	Chrysomelidae sp 4	1	5	2
Coleoptera	Coccinellidae			
	Coccinellidae sp 1	1	5	2
	Coccinellidae sp 2	1.14 ± 0.14	17.5	8
Coleoptera	Scarabaeidae			
	Scarabaeidae sp 1	1	2.5	1
Diptera	Culicidae			
	Culicidae sp 1	1.31 ± 0.13	32.5	17
	Dryinidae			
	Dryinidae sp 1	1	10	4
Hemiptera	Aphididae			
	Tuberolachnus salignus	3 ± 2	5	6
Hemiptera	Pentatomidae			
	Pentatomidae sp 2	1	2.5	5
Hemiptera	Psyllidae			
	Helionidia quadrimaculata	1.82 ± 0.29	42.5	31
Hymenoptera	Braconidae			
	Chrysopidae sp 2	1	5	2
Hymenoptera	Formicidae			
	Formicidae sp 1	1.09 ± 0.09	27.5	12
	Ichneumonidae			
	Ichneumonidae sp 1	1	2.5	1
	Ichneumonidae sp 2	1	2.5	1
	Noctuidae			
	Noctuidae sp 1	1	2.5	1
Hymenoptera	Tenthredinidae			
	Nematus oligospilus	1	12.5	5
	Nematus oligospilus (larvae)	1.8 ± 0.41	25	18
	Tenthredinidae sp 2	1	2.5	1
Lepidoptera	Crambidae			
	Crambidae sp 1	1	5	2
Neuroptera	Chrysopidae			
	Chrysopidae sp 2	1	5	2
Psocoptera	Psoidae			
	Psoidae sp 1	1	20	8

References

Barkat H, War AR, Singh S, Ahmad S (2021) First record of an invasive pest, Giant Willow Aphid, *Tuberolachnus salignus* (Gmelin) (Hemiptera: Aphididae) on *Salix alba* in the cold arid region of Ladakh, India. Entomol News 129(5):538–545

Branco M, Brockerhoff EG, Castagneyrol B, Orazio C, Jactel H (2015) Host range expansion of native insects to exotic trees increases with area of introduction and the presence of congeneric native trees. J Appl Ecol 52(1):69–77

Brockerhoff EG, Liebhold AM (2017) Ecology of forest insect invasions. Biol Invasions 19:3141–3159

CARA (1983) Conservation of Agricultural Resources Act, 1983 (Act No. 43 of 1983). Government Gazette No. 8806. Pretoria: Government Printer, South Africa

Caron V, Moslih F, Ede F, O'Dowd DJ (2011) An accidental biological control agent? Host specificity of the willow sawfly *Nematus oligospilus* (Hymenoptera: Tenthredinidae) in Australia. Aust J Entomol 50:290–295

Crawley MJ (1997) Plant ecology. Blackwell, Oxford

Crous CJ, Burgess TI, Le Roux JJ, Richardson DM, Slippers B, Wingfield MJ (2016) Ecological disequilibrium drives insect pest and pathogen accumulation in non-native trees. AoB Plants. https://doi.org/10.1093/aobpla/plw081

Davy JB (1922) The distribution and origin of *Salix* in South Africa. J Ecol 10(1):62–86

De Tillesse V, Nef L, Charles J, Hopkin A, Augustin S (2017) Damaging poplar insects: internationally important species. The Food and Agriculture Organization of the United Nations, Rome

Deus E, Silva JS, Catry FX, Rocha M, Moreira F (2016) Google street view as an alternative method to car surveys in large-scale vegetation assessments. Environ Monit Assess 188:1–14

Duso C, Skuhravá M (2002) First record of *Obolodiplosis robiniae* (Haldeman) (Diptera Cecidomyiidae) galling leaves of *Robinia pseudacacia* L. (Fabaceae) in Italy and Europe. Frustula Entomol 25:117–122

Dworakowska I (1992) A review of the genus *Helionidia* Zachvatkin and supplement of *Empoascanar* Distant (Auchenorrhyncha, Cicadellidae, Typhlocybinae, Erythroneurini). Folia Entomol Hung 53:17–44

Forister ML, Novotny V, Panorska AK, Baje L, Basset Y, Butterill PT, Cizek L, Coley PD, Dem F, Diniz IR, Drozd P (2015) The global distribution of diet breadth in insect herbivores. In: proceedings of the national academy of sciences, 112(2), pp. 442–447.

GBIF Global Biodiversity Information Facility [WWW Document] 2024 Available online: https://www.gbif.org/species/5372639. Accessed 6 May 2024

Gougherty AV, Davies TJ (2021) Towards a phylogenetic ecology of plant pests and pathogens. Philos Trans R Soc Lond B Biol Sci 376:20200359

Gutierrez AP, Ponti L (2013) Prospective analysis of the geographic distribution and relative abundance of Asian citrus psyllid (Hemiptera: Liviidae) and citrus greening disease in North America and the Mediterranean basin. Fla Entomol 96:1375–1391

Gwate O, Dlomu MG, Toucher M, le Roux PC, Martin GD, Clark VR (2024) Endemic darling or global change menace? A review of the woody encroacher *Leucosidea sericea* on the eastern great escarpment of southern Africa. S Afr J Bot 174:307–317

Helbig CE, Müller MG, Landgraf D (2021) Effects of leaf loss by artificial defoliation on the growth of different Poplar and Willow varieties. Forests 12(9):1224

Henderson L (1991) Alien invasive Salix spp. (willows) in the Grassland Biome of South Africa. S Afr for J 157(1):91–95

Henderson L (2007) Invasive, naturalized and casual alien plants in southern Africa: a summary based on the southern African plant invaders atlas (SAPIA). Bothalia 37(2):215–248

Henderson L (2020) A complete guide to declared weeds and invaders in South Africa, including another 40 taxa invasive in that region. Plant Prot Res Inst Handb 21:228

Hurley BP, Garnas J, Wingfield MJ, Branco M, Richardson DM, Slippers B (2016) Increasing numbers and intercontinental spread of invasive insects on eucalypts. Biol Invasions 18(4):921–933

Immelman WFE (1973) Our green heritage: a book about Indigenous and exotic trees in South Africa, about trees and timber in our cultural history and about our extensive silvicultural forestry and timber industries. Tafelberg, Cape Town

Immelman KL (1987) Synopsis of the genus *Salix* (Salicaceae) in southern Africa. Bothalia 17(1):171–177

Impson FAC, Kleinjan CA, Hoffmann JH, Mudavanhu P (2021) A review of research and developments with insect agents used for biological control of Australian *Acacia* species (Caesalpinioideae) in South Africa. Afr Entomol 29(3):693–712

Impson FAC, Hoffmann JH, Impson OR, Kleinjan CA, Moran VC (2024) Densities of a perennial invasive tree, *Acacia cyclops*, decline in the 20 years since inception of biological control with two seed-reducing agents, a flower-galling midge and a seed-feeding weevil. Biol Control 189:105442

Karrenberg S, Edwards PJ, Kollmann J (2002) The life history of Salicaceae living in the active zone of floodplains. Freshwater Biol 47(4):733–748
Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. Trends Ecol Evol 17(4):164–170
Klein RM, Link GK (1955) The etiology of crown-gall. Q Rev Biol 30(3):207–277
Kotzé JD, Wannenburgh A, van Wilgen BW (2025) Changes in the cover of selected invasive alien plant taxa between 2008 and 2023 in South Africa. Biol Invasions 27(3):1–17
Liebhold AM, Brockerhoff EG, Kalisz S, Nuñez MA, Wardle DA, Wingfield MJ (2017) Biological invasions in forest ecosystems. Biol Invasions 19(11):3437–3458
Malagón-Aldana LA, Serna F, Smith DR (2017) On the natural history of the willow sawfly *Nematus oligospilus* (Hymenoptera, Tenthredinidae) inhabiting *Salix humboldtiana*, in Colombia. J Hymenopt Res 55:189–199
Martin GD (2019) Addressing geographical bias: a review of *Robinia pseudoacacia* (black locust) in the Southern Hemisphere. S Afr J Bot 125:481–492
Martin GD (2021) Prospects for the biological control of Northern temperate weeds in South Africa. Afr Entomol 29(3):791–808
McFadyen REC (1998) Biological control of weeds. Annu Rev Entomol 43(1):369–393
Medzihorský V, Mally R, Trombik J, Turčáni M, Medzihorská M, Shoda-Kagaya E, Martin GD, Sopow S, Kochi K, Liebhold AM (2024) The demise of enemy release associated with the invasion of specialist folivores on an invasive tree. Ecography 2024(5):e07082
Moran VC, Hoffmann JH, Hill MP (2011) A context for the 2011 compilation of reviews on the biological control of invasive alien plants in South Africa. Afr Entomol 19:177–185
Mucina L, Rutherford MC (2006) The vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria
Core Team R (2023) R: A language and environment for statistical computing. R foundation for statistical computing, Vienna, Austria. <https://www.R-project.org/>.
SANBI (2013) Grasslands ecosystem guidelines: landscape interpretation for planners and managers. Compiled by Cadman M, de Villiers C, LechmereOertel R, McCulloch D. South African National Biodiversity Institute, Pretoria.
Sheppard AW, Shaw RH, Sforza R (2006) Top 20 environmental weeds for classical biological control in Europe: a review of opportunities, regulations, and other barriers to adoption. Weed Res 46:1–25
Simberloff D, Gibbons L (2004) Now you see them, now you don't! Population crashes of establishedintroduced species. Biol Invas 6:161–172
Skowno AL, Thompson MW, Hiestermann J, Ripley B, West AG, Bond WJ (2017) Woodland expansion in South African grassy biomes based on satellite observations (1990–2013): general patterns and potential drivers. Glob Change Biol 23(6):2358–2369
Spiers AG (1980) Biological control of Agrobacterium species on *Salix*. N Z J Agric Res 23(1):139–142
Sprecher-Uebersax E, Daccordi M (2016) Leaf-beetles of the subfamily Chrysomelinae of Laos (Coleoptera: Chrysomelidae). Entomologica Basiliensia Et Collectionis Frey 35:455–485
Strong DR, McCoy ED, Rey JR (1977) Time and the number of herbivore species: the pests of sugarcane. Ecology 58:167–175
Teshome DT, Zharare GE, Naidoo S (2020) The threat of the combined effect of biotic and abiotic stress factors in forestry under a changing climate. Front Plant Sci 11:601009
Theron JG (1977) The Naudé species of South African Cicadellidae, Hemiptera, part 6. Some species assigned to the genera *Erythroneura* and *Empoasca*. J Entomol Soc South Afr 40(1):109–118
Toome M, Aime MC (2015) Reassessment of rust fungi on weeping willows in the Americas and description of *Melampsora ferrinii* sp. nov. Plant Pathol 64(1):216–224
Urban AJ, Eardley CD (1995) A recently introduced sawfly, *Nematus oligospilus* Forster (Hymenoptera: Tenthredinidae), that defoliates willows in southern Africa. Afr Entomol 3(1):23–27
Vacek Z, Vacek S, Cukor J (2023) European forests under global climate change: review of tree growth processes, crises and management strategies. J Environ Manage 332:117353
Van Splunder I, Coops H, Voesenek LACJ, Blom CWPM (1995) Establishment of alluvial forest species in floodplains: the role of dispersal timing, germination characteristics and water level fluctuations. Acta Bot Neerl 44(3):269–278
Wingfield MJ, Brockerhoff EG, Wingfield BD, Slippers B (2015) Planted forest health: the need for a global strategy. Science 349(6250):832–836
Wood AR, Morris MJ (2007) Impact of the gall-forming rust fungus *Uromycladium tepperianum* on the invasive tree *Acacia saligna* in South Africa: 15 years of monitoring. Biol Control 41(1):68–77
Zachariades C (2021) A catalogue of natural enemies of invasive alien plants in South Africa: classical biological control agents considered, released and established, exotic natural enemies present in the field, and bioherbicides. Afr Entomol 29(3):1077–1142