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Direct and Indirect Impacts of the *Tuberolachnus salignus* (Hemiptera: Aphididae) Invasion in New Zealand and Management Alternatives

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Abstract

Invasive insects are a serious problem in New Zealand, and their introduction and successful establishment are predicted to increase with global commerce and climate change. A recent introduction to New Zealand is *Tuberolachnus salignus* (Gmelin), a large aphid that attacks mainly willows but also other plants such as poplars, apples, and pears. It was first reported in 2013 but has since then spread rapidly throughout the country. We conducted a 2-yr study exploring the direct (on the host plant) and indirect (on other organisms) impacts of the aphid, in a field setting including 15 willow clones selected to represent the variety of species and hybrids present in New Zealand. Our research revealed great variation in the level of resistance/susceptibility of different clones and suggested a trade-off between reproduction, growth, and defense. We investigated the indirect effects of the aphid on honeydew foragers and on the soil ecosystem, through honeydew production and deposition, revealing complex cascading effects involving multiple trophic levels. We also explore and discuss management alternatives including the replacement of willows for native species or resistant varieties, the use of biological control agents, and the feasibility of chemical control. This work is one of few studies on the complex ecological effects of invasive phytophagous insects and could serve as a model for future research and to inform pest management. To conclude, we identify gaps in the knowledge and highlight aspects requiring further research.

Key words: invasive species, ecological impact, insect–plant interaction, biological control, *Salix*

Invasive alien species are those that have been introduced to areas outside their native range (typically as result of human activity), are able to reproduce and sustain large populations over time, and have a negative impact (economic, social, health, ecological or environmental) on the areas they invade (IUCN 2000). New Zealand is, after the United States, the country with the second highest number of invasive species per unit area in the world, with nearly 125 invasive species per 100,000 km^2 (Turbelin et al. 2017). Due to the unique evolutionary history of New Zealand, resulting from its early split from Gondwana, and high levels of endemism, it is arguably one of the most vulnerable regions in the world to the impacts of invasive species (PCE 2021).

One of the most recent alien insect introductions to New Zealand is the aphid *Tuberolachnus salignus* (Gmelin). This species is thought to be of Asian origin and was first reported in New Zealand in 2013, spreading rapidly through the country where it attacks multiple plant species, predominantly willows (*Salix* spp., Salicacea), and, in lesser proportion, poplars, apples, and pears. These are very large aphids that form dense clusters on the tree trunks or branches (Fig. 1), where they feed on phloem sap and produce copious amounts of honeydew (Sopow et al. 2017). They are fully parthenogenetic, and infestation occurs by the dispersal of alate aphids during spring, summer, and autumn, with populations of apterous aphids increasing in spring and summer, peaking in autumn, and declining in winter (Jones et al. 2021).

Willows are non-native to New Zealand and are comprised of a variety of species and cultivars (Harman 2004). Although a few species such as *Salix cinerea* L. and *Salix fragilis* L. are considered weeds (Harman 2004), most species are seen as desirable plants and used for a variety of purposes including riverbank stabilization (van Kraayenoord et al. 1995), soil erosion control (Wilkinson 1999), forage (Kemp et al. 2001), and as a source of pollen for overwintering honeybees (Newstrom-Lloyd 2015), while others are commonly planted for their aesthetic value (Harman 2004). Given the multiple uses of willows in New Zealand, the aphid infestation has been linked to a variety of negative economic impacts, mainly for the farming and

Fig. 1. *Tuberolachnus salignus* cluster feeding on a willow branch (photograph credit: John McLean).

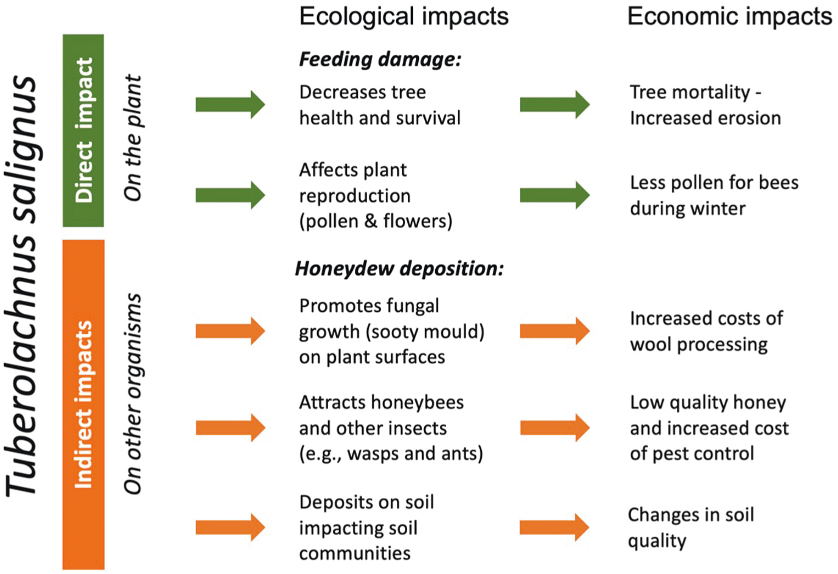

Fig. 2. Relationship between ecological and economic impacts associated with the *Tuberolachnus salignus* invasion in New Zealand.

apiculture industries. Some impacts are directly related to declining plant health and increased mortality, e.g., the need to replace plants used for erosion control and riverbank stabilization. However, in many cases, the impacts are indirect, i.e., on other organisms associated with honeydew deposition. Examples of indirect impacts include increased costs in wool processing due to sheep getting covered in aphid honeydew, production of low quality (cement) honey because of honeybees feeding on the honeydew, and increased costs of pest control due to non-native *Vespula* (Hymenoptera: Vespidae) wasps being attracted to the honeydew (Sopow 2017). Many of these economic impacts can be traced back to the disruption of ecological processes (Fig. 2). However, although economic impacts of invasive insects are often measured and quantified, the ecological impacts are rarely explored and poorly understood (Kenis et al. 2009).

With the aim of exploring the direct and indirect ecological impacts of this invasive insect and management alternatives, a field trial was set up using 15 common willow clones including different growth forms (shrubs and trees), sex (male or female), and geographical origins (Table 1). Willows, derived from clonal cuttings, were planted in six rows (12 plants per clone per row), with two treatments (3 aphid-infested rows and 3 aphid-uninfested rows; Fig. 3; for experimental setup see Tun et al. 2020a). We followed the growth of the plants for 2 yr (2017–2019) and measured various parameters in relation to aphid infestation: direct impacts on plant survival, growth, reproduction, and defense (i.e., emission of volatile organic compounds [VOCs]), and indirect impacts, related to honeydew deposition, on other organisms (e.g., soil microorganisms and microarthropods) and the environment (e.g., soil

Table 1. List of willow cultivars used in the field trial

Species/hybrid/clone	Geographical origin	Type	Sex	Susceptibility to the aphid[a]
S. candida Flüggé ex Willd	North America	Shrub	Male	Highly susceptible
S. eriocephala Michx	North America	Shrub	Male	Resistant
S. lasiolepis Benth	North America	Shrub	Male	Susceptible
S. lasiolepis × *S. viminalis*	Hybridized in New Zealand	Shrub	Male	Resistant
*S. purpurea*L.	Europe, North Africa	Shrub	Female	Moderately resistant
S. schwerinii E. Wolf	Eastern Asia	Shrub	Male	Highly susceptible
*S. viminalis*L.	Europe, Western Asia	Shrub	Male	Highly susceptible
S. × *reichardtii*[b]	Europe	Shrub	Male	Susceptible
*S. alba*L.	Europe, Western and Central Asia	Tree	Male	Susceptible
S. lasiandra Muhl	North America	Tree	Male	Moderately resistant
S. matsudana Koidz	Eastern Asia	Tree	Female	Susceptible
S. matsudana × *S. alba*(clone 1)	Hybridized in New Zealand	Tree	Female	Highly susceptible
S. matsudana × *S. alba*(clone 2)	Hybridized in New Zealand	Tree	Male/female	Highly susceptible
S. matsudana × *S. lasiandra*	Hybridized in New Zealand	Tree	Male	Susceptible
S. × *fragilis*[c]	Europe and Western Asia	Tree	Female	Susceptible

[a] Measured as the number of weeks with sustained high population levels, according to Tun et al. (2021b).

[b] *S.* × *reichardtii* is a hybrid between *S. caprea* and *S. cinerea* (Glenny and Jones 2019).

[c] *S.* × *fragilis* is a hybrid between *S. euxina* and *S. alba* (Glenny and Jones 2019).

Fig. 3. Field trial setting conducted at the Plant Growth Unit of Massey University in Palmerston North, Manawatu, New Zealand (photograph credit: Kyaw Min Tun).

properties and enzymes related to nutrient cycling). In this case study, we summarize the outcomes of these observations and identify gaps in the knowledge to guide future research. We hope this study can serve as a model to investigate the ecological impacts of other established invasive insects and to identify suitable strategies for their management.

Direct Impacts

Plant Survival, Growth, Reproduction, and Defense

Herbivory has an impact on the survival, growth, and reproduction of plants (biological fitness; Hendrix 1988; Herms and Mattson 1992). Plants have evolved different mechanisms to avoid, tolerate or recover from herbivory. Avoidance involves an investment in defense structures or chemical compounds to reduce the probability and intensity of herbivory; tolerance is the degree to which a plant can support a given insect population in comparison to a susceptible plant and is linked to the presence of resistance genes. Finally, recovery involves mechanisms to increase plant growth or reproduction following herbivory such as meristem availability and other physiological processes (Briske 1996; Thomas and Waage 1996). Since there is a cost associated with each of these strategies, trade-offs are expected to occur favoring one strategy over another (Tuller et al. 2018).

The willow clones in the field trial varied widely in their susceptibility to infestation (Table 1). Highly susceptible willows such as *S. candida* and *S. viminalis* hosted larger populations of apterous aphids for longer periods (>100 individuals for more than 12 wk), whereas resistant clones *S. eriocephala* and *S. lasiolepis* × *S. viminalis* did not sustain high populations (<100 individuals) during the experiment (Jones et al. 2021). The willow species most susceptible to aphid infestation also experienced lower survival of aphid-infested plants (Jones et al. 2021). This occurred during the second year, with the willow plants failing to commence growth in the spring.

The aphids appear to have depleted the willows of nutrients in the autumn, when the plants need to store starch reserves to survive the winter and to commence growth and flowering in the spring. The depletion of carbohydrate reserves in autumn has been observed with *Phloeomyzus passerinii* Signoret (Hemiptera: Aphididae) infestation of *Populus tremuloides* Michx (Salicaceae) and has been associated with tree mortality (Sallé et al. 2018).

The aphids had no effect on the growth of the willow plants in the first year, but there was a reduction in the stem and root growth of the aphid-infested willow plants during the second year, with reductions in stem and root biomass growth of 20–49% in willows commonly used for soil conservation in New Zealand (*S. purpurea*, *S. schwerinii*, *S. viminalis*, *S. matsudana*, and *S. matsudana* × *alba*; Jones et al. 2021). Interestingly, aphid infestation had a seemingly positive effect on plant reproduction, observed as a delayed and extended flowering period and a reduction in size but higher number of flowering catkins in the spring of the second year. We found an increase in the total floral output of infested plants when compared with noninfested ones (Tun et al. 2021b). Compensatory growth and reproduction are well-known plant recovery mechanisms (McNaughton 1983; Hendrix 1988); however, the ability of individual plants to compensate will be strongly linked to their tolerance to a particular herbivore and the available resources on the environment (Wise and Abrahamson 2005) and thus may vary between plants (especially if these are nonclonal) and sites.

Plant defenses against herbivores (avoidance mechanisms) can be mechanical (such as thorns, trichomes, or waxes) or chemical (secondary metabolites or specialized defense proteins). Chemical defenses can be either constitutive (present at all times) or induced (produced or released in response to herbivore attack), and direct (having a direct impact on the herbivore acting as toxins, deterrents, or repellents) or indirect (affecting the herbivore by attracting its natural enemies; Arimura et al. 2005). While these traits are genetically determined due to the environment and co-evolutionary history with the herbivores, different biotic and abiotic parameters can affect the plants' phenotype (phenotypic plasticity; Ballhorn et al. 2011). Volatile organic compounds (VOCs) are a good example of plant chemical defenses, being both constitutive and induced, having direct and indirect properties, and displaying high phenotypic plasticity (Clavijo McCormick et al. 2012; Clavijo McCormick 2016).

We measured the VOCs of the 15 willow clones, with and without aphid infestation. Volatiles were collected using a headspace sampling method and analyzed using gas chromatography–mass spectrometry. We found high variability in the volatile profiles of different species and hybrids, suggesting differences in their chemical defenses. However, taxonomically related plants showed an overlapping pattern of VOC emission, and there seemed to be a clear separation between shrub and tree willows (Tun et al. 2020c). Interestingly, aphid infestation did not have a significant effect on the VOC profiles of most willow species, with only four clones (*S.* × *reichardtii*, *S. matsudana* × *S. lasiandra*, *S. matsudana* × *S. alba*, and *S. candida*) showing a significant response (decrease in VOC emission) in response to aphid infestation. We propose various explanations, which may not be mutually exclusive, for this response or the lack of it: 1) plants may be unable to respond efficiently to invasive insects they have not coevolved with (Desurmont et al. 2014), 2) *T. salignus* does not damage photosynthetically active tissue where secondary metabolites are produced (Turlings et al. 1998), 3) aphid symbionts could attenuate the induction of plant VOCs as observed in other systems (Frago et al. 2017), or 4) there can be trade-offs between the emission of volatiles and other forms of plant defense, or between defense and growth/reproduction (Rudgers et al. 2004), which is likely due to the observed increase in reproductive potential, linked to reduced growth. Further research is needed to elucidate the impact of *T. salignus* on plant defense responses, and the trade-offs between growth, reproduction, and defense in these willow clones.

Indirect Impacts

Honeydew Production, Composition, and Its Impact on Honeydew-Foraging Insects

Tuberolachnus salignus takes up a large quantity of phloem sap from willow stems/branches through their proboscis and, as a result, deposits copious amounts of unassimilated sap in the form of honeydew (Sharma et al. 1995). At their high population density, honeydew deposition feels like a light shower while standing under the canopy of infested trees (Sopow 2016b). In a study conducted in the United Kingdom, Mittler measured the honeydew excretion of *T. salignus* apterous adult aphids fed on *S. acutfolia* Willd under controlled conditions and found that a single aphid can excrete between 1.71 and 2.06 mm^3/h (Mittler 1957). Chemically, aphid honeydew is a viscous liquid, consisting mainly of sugars with a small fraction of amino acids, and other insect- and plant-derivative compounds (Hussain et al. 1974; Blüthgen et al. 2004; Dhami et al. 2011). The phloem sap of willows contains only one disaccharide, sucrose, that is synthesized into a trisaccharide melezitose in the aphid's gut (Mittler 1958). Honeybees (Apis mellifera L., Hymenoptera: Apidae) forage on *T. salignus* honeydew during spring and summer. Melezitose, an indigestible sugar for honeybees, can negatively impact their health and easily crystallize in the comb, causing difficulties in honey extraction (Imdorf et al. 1985; Howse 2017; Sopow et al. 2017; Seeburger et al. 2020). Honeydew feeding by honeybees was also reported to decrease both the quantity and quality of honey products (Sopow et al. 2017).

In our field experiment, we used mesh-covered plastic cups (7.5 cm diameter, 10 cm height; Fig. 4) that were attached with a

Fig. 4. A wasp (a) and a honeybee (b) foraging honeydew from a collection cup (photograph credit: Kyaw Min Tun).

wire to tree branches and stems below aphid colonies to collect honeydew. Honeydew could not be harvested from resistant clones (*S. eriocephala* and *S. lasiolepis* × *S. viminalis*) when we collected it at the aphid's peak population density in 2018 and 2019. Compared to *S. lasiolepis* × *S. viminalis*, on which the aphids excreted very few droplets, *S. eriocephala* seemed to be less preferable and more resistant, with no sign of honeydew deposition on it. The lack of honeydew on resistant clones might be due to their hard bark, which acts as a mechanical barrier making the aphid stylet difficult to insert into the phloem. Under the canopy of the most susceptible clones (*S. viminalis*, *S. candida*, and *S. schwerinii*), honeydew deposition was abundant, and black sooty mold areas were prevalent on the foliage and soil surface. The amount of honeydew deposition also varied with the resistance levels of the host willows, on which the aphids fed (unpublished data).

We used high-performance liquid chromatography to determine how willow clones and plant age (first- and second-year willow) influence the content of melezitose and related sugars in the excreted aphid honeydew. Melezitose was the most abundant sugar in the honeydew, ranging from 56.72 to 84.20 g/l and was not significantly different between plant clones (Tun et al. 2021a). In contrast, other sugars (monosaccharides and disaccharides) were less abundant and significantly influenced by the clone and plant age. Sucrose content ranged from 11.99 to 46.40 g/l, fructose content from 14.87 to 19.46, and glucose content from 0.08 to 4.31 g/l (Tun et al. 2021a). This variation can be explained by the difference in the sucrose content in the phloem sap of willow clones (Fischer and Shingleton 2001) and the physiological state of host plants (sampling years/plant age; Beggs et al. 2005). Melezitose content has been shown to be strongly linked to the activity of insect gut microbes and enzymes that help hydrolyze sucrose into melezitose after its consumption, which might explain its high abundance and low variation among clones (Wolf and Ewart 1955). Information on gut microbiota enzymes is still lacking for *T. salignus*. Further research is also needed to explore seasonal variation in the melezitose concentration in *T. salignus* honeydew, the melezitose content associated with other willow clones and poplars (known as their alternative hosts), and the effect of other environmental and biological factors governing honeydew production and sugar concentration. The impact of *T. salignus* honeydew consumption on honeybee health and honey production also needs further assessment.

Tuberolachnus salignus honeydew provides an energy-rich food source, attracting not only honeybees but other insects such as wasps, flies, and ants (Sopow et al. 2017). Their busy activities and buzzing indicate aphid presence on willow trees and signal that the aphids are depositing honeydew (Cameron et al. 2019). In the New Zealand willow system, *T. salignus* and its honeydew are responsible for the increased population of *Vespula* wasps, causing an additional problem in apiculture as the wasps steal honey from hives and attack the honeybees (Lester et al. 2013; Sopow 2016a). In our willow field trial, ants also collected honeydew, reducing the amount falling on the leaves and branches of infested willow trees, especially at the beginning of the population buildup. There could be a trade-off between the populations of ants and wasps, with the absence of ants contributing to increased honeydew availability for the wasps (Dransfield and Brightwell 2015). Honeydew also serves as a foraging cue and alternative food source for ladybird beetles, parasitoids, and other predators that feed on the aphid (Douglas 2009), so it could also contribute to the recruitment of natural enemies of the aphid and promote the activity of biocontrol agents.

Honeydew Deposition on Soil and Its Impact on Soil Properties and Soil Biota

A large proportion of the *T. salignus* honeydew falls directly on the soil surface under the canopy of infested plants. One of the characteristic features of aphid infestation is the growth of black sooty mold on the soil and other surfaces (Fig. 5). Aphid honeydew provides a readily available food source for soil microorganisms, resulting in an increase in microbial activity and biomass that consequently lead to a change in soil chemical properties and affect other soil biota through a trophic cascade (Sinka et al. 2009; Torres et al. 2015).

Fig. 5. The arrow points to the growth of sooty mold on the soil surface due to *Tuberolachnus salignus* honeydew deposition (photograph credit: Kyaw Min Tun).

Aphid herbivory and the associated deposition of sugary honeydew are known to affect soil nutrient availability through their influence on soil microbial populations (Owen and Wiegert 1976; Owen 1980; Petelle 1980; Stadler et al. 2006). Soil microbial populations are assumed to be energy limited (Blagodatskaya and Kuzyakov 2013) and are stimulated by the addition of labile C sources. Sugar supplementation encourages soil microbes to become active and produces a significant increase in microbial biomass, basal respiration rate, and microbial metabolic activity (associated with enzyme production) and diversity (Shi et al. 2011). The high C:N ratio of the honeydew means that it provides a rich source of available C but only a limited amount of N to growing soil microbial populations (Choudhury 1985; Chen et al. 2014; Jílková et al. 2018). It has been hypothesized that enhanced microbial activity, stimulated by honeydew deposition, may result in decreased soil N availability and have a negative effect on host plants, as microorganisms compete with host plants for limited N resources (Dighton 1978; Stadler et al. 2008). On the other hand, there is also evidence that sugar supplementation increases soil N availability, which has been attributed to the increase in soil N-fixation by non-symbiotic bacteria (Owen and Wiegert 1976; Petelle 1980; Stadler et al. 2006). Some microbial taxa can be negatively affected by honeydew sugars (Islam and Wright 2004), but studies exploring the functional response of soil microbes to honeydew deposition are scarce (Michalzik et al. 1999).

In this 2-yr field trial, we explored the effect of *T. salignus* honeydew deposition on soil properties (C, N, and C:N ratio), soil microbial biomass, soil yeasts, soil enzymes, and mesofauna (Tun et al. 2020a). We took soil samples using a 25 cm^2 rectangular soil corer at the depth of 5 cm before planting the trees as a reference, and then after 1 and 2 yr. Soil samples were taken from clean areas (without sooty mold) under the tree canopy of aphid-infested and control rows. Since black sooty mold spots on the soil surface are characteristic of honeydew deposition, we also collected soil samples directly underneath these spots for analysis (for experimental setup, see Tun et al. 2020a). Six enzymes were selected based on their sensitivity and importance in the electron transport system (dehydrogenase), cycling of C (glucosidase, invertase, and amylase), and N (amidase and urease). The activity of soil enzymes reflects the metabolic response of the soil microbial communities to changes in nutrient availability (García-Ruiz et al. 2008) and is a sensitive bioindicator for subtle changes in soil quality and resources (Torres et al. 2015). We hypothesized that *T. salignus* honeydew deposition on the soil surface will increase soil microbial biomass and activity, influence soil properties and nutrient availability, and affect soil mesofauna (Stadler et al. 2006; Rousk et al. 2009).

As expected, we found that the deposition of *T. salignus* honeydew on the soil surface affected the soil biological and biochemical properties. Aphid infestation significantly increased microbial biomass C, basal respiration, number of yeast colony-forming units, and the activity of soil enzymes, with the highest effect under the black sooty mold spots (Tun et al. 2020a). The microbial biomass C was positively correlated with the soil total C content and negatively correlated with the total N content, reflecting microbial C:N balance requirements (Johnson et al. 2005; Cheng et al. 2013). The activities of all six assayed enzymes were positively correlated with microbial biomass C, especially β-amylase, urease, and dehydrogenase. Dehydrogenase, especially, is a sensitive indicator of increased microbial activity and microbial biomass (García-Ruiz et al. 2012; Ruzhen et al. 2014).

The increase in soil C content was significant, but less pronounced outside of the black sooty mold spots. There was no effect on the soil pH values or total N content (Tun et al. 2020a). Interestingly, contrary to published sources (Owen and Wiegert 1976; Petelle 1980; Stadler et al. 2006), we found that *T. salignus* honeydew deposition did not change soil total N content. No information is currently available on to what extent honeydew deposition can change soil nitrogen fixation and which functional groups of microbes may be affected. Further studies using molecular techniques are advised to determine the changes in the soil microbial community due to honeydew deposition and to assess the long-term effects of honeydew deposition on soil nutrient availability and on the productivity of host plants.

Soil mesofauna extraction was done using a modified Berlese-Tullgren apparatus in a temperature-controlled room for 7 d (Tun et al. 2020a). It was observed that Collembola was the most abundant group, followed by Gamasida, Astigmata, and Oribatida. The number of individuals per square meter was significantly higher for Collembola, Gamasida, and Astigmata in the sooty mold spots during the first year. Collembola, Astigmata, and Oribatida are fungivores and detritivores, whereas Gamasida are predators of the other groups (Koehler 1999; Schneider et al. 2004; Gan et al. 2014). Therefore, our results suggest that honeydew deposition directly increased the abundance of Collembola and Astigmata through augmented microbial biomass, and indirectly increases the abundance of Gamasida, due to higher availability of their prey. The results provide evidence that *T. salignus* herbivory can trigger a cascading effect on the soil biotic community, modifying ecological interactions and nutrient cycling in the willow system.

Management Alternatives

In New Zealand, different regions are considering replacing willows for native species for streambank control, this would be useful to manage *T. salignus* populations and reduce their spread. Some replacement initiatives predate the introduction of *T. salignus* to New Zealand, and mainly relate to the fact that some non-native willows are seen as a threat to native species and freshwater ecosystems and to the weedy behavior of species such as *S. fragilis* and *S. cinerea*, which form dense stands of unstable trees with large root mats producing lots of debris, leading to waterway blockage and infrastructure damage (Philips and Daly 2008). However, willow replacement for natives is not always feasible due to 1) the extent of use of the species and costs involved (e.g., the Wellington region invested 9.2 million NZD in 2000, for an erosion control and riverbank stabilization programme using willows) and 2) there are few native species having the same properties as willows (deep roots, rapid growth, vegetative cuttings, etc.) making them less suitable for the same uses. For instance, there are no available alternatives to willows that can give the required level of flood protection in aggressive systems such as gravel systems, which are common in New Zealand (Harman 2004). Therefore, willows are likely to continue being used against soil erosion and for riverbank protection. In our trial, we encountered two resistant clones *S. eriocephala* and *S. lasiolepis* × *S. viminalis* that did not sustain high populations of aphids (Jones et al. 2021) and from which no honeydew was recovered (Tun et al. 2021a). *Salix eriocephala* has shown to be useful in riverbank stabilization in other countries like Canada (Bariteau et al. 2013) and is not known to display weed-like behavior in New Zealand, making it a promising alternative. The use of *S. lasiolepis* × *S. viminalis* for this purpose remains to be assessed. The replacement of susceptible for more resistant clones could be a useful tool to reduce and manage aphid infestation, but further research is required to explore and develop new resistant willow varieties.

Another management alternative is the use of biological control agents, which could involve the use of organisms already existing in the area or the introduction of specialized natural enemies from the native range. In our field study, we often observed a generalist predator, the multicolored Asian ladybird beetle *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae), foraging on *T. salignus* and its honeydew. *Harmonia axyridis* had been previously reported as a potential predator of *T. salignus* in New Zealand (Sopow et al. 2017), but its suitability as biocontrol agent was unclear since it was not known if the aphid was a preferred food source and the aphid's suitability for the ladybird's development and reproduction. Therefore, we conducted a laboratory trial to explore these questions. Our study confirmed that *H. axyridis* can predate and survive on the early instars of *T. salignus* although the ladybird survival is lower, body weight is lighter and development periods are more extended, compared to those fed with a standard rearing diet consisting of frozen eggs of the Mediterranean flour moth *Ephestia kuehniella* Zeller (Lepidoptera: Pyralidae) (Tun et al. 2020b). However, *H. axyridis* was not recommended as a potential biocontrol agent due to its high voracity and lack of host specificity. In our study, the multicolored Asian ladybird beetle showed a significant preference for *Myzus persicae* Sulzer (Hemiptera: Aphididae)—green peach aphids—when these were offered in a two-choice assay alongside *T. salignus* (Tun et al. 2020b). Recently, host testing for the specialized parasitoid *Pauesia nigrovaria* Provancher (Hymenoptera: Braconidae: Aphidiinae) was conducted to explore the safety of its potential introduction to New Zealand (Sopow et al. 2021). The results show that this parasitoid is highly host specific and that its introduction to New Zealand poses a negligible risk, suggesting that this is a better alternative for biological control.

Entomopathogenic fungi are well-known biological control agents against aphids (Shah and Pell 2003; Hong and Kim 2007; Khan et al. 2012). The fungal pathogen, *Neozygites turbinata* (R. G. Kenneth) Remaud. & S. Keller (Zygomycetes: Entomophthorales), has been reported to kill *T. salignus* in other countries (United Kingdom, Slovakia, Israel, United States, and Canada) having a significant impact on aphid populations (Kenneth 1977; Barta & Cagáň 2006; Aradottir 2010; Montalva et al. 2014). However, *N. turbinata* is not present in New Zealand, and it is unlikely to be introduced as a biological control agent due to its unknown host specificity that would require extensive testing, and to challenges associated with its isolation and persistence in nature (Sopow et al. 2017). Testing entomopathogens already present in New Zealand against *T. salignus*, such as the closely related *N. fumosus* (Speare) Remaud. & S. Keller [as 'fumosa'] [nom. inval.] and *N. parvispora* (D.M. MacLeod & K.P. Carl) Remaud. & S. Keller could be an opportunity for future research (Landcare Research 2016).

The use of chemical control (insecticides) has poor social acceptance and is not feasible at a large scale due to the reliance of the New Zealand apiculture industry on willows and the risk to native insects. However, it may be used at a local scale (e.g., city parks or residential settings), where secondary problems such as the attraction of wasps pose a threat to human health (Sopow et al. 2017).

Conclusions and Outlook

The case of *T. salignus* illustrates the importance of multitrophic interactions involving invasive species. Not only do invasive phytophagous insects affect their potential hosts plants, but also their environment and the ecological communities around them. Our study revealed that plants within the same genus can vary greatly in their resistance to invasive insects, but there are some observable trends. In this case, willow plants favored compensatory reproduction as a strategy to overcome an invasive attacker, but at the cost of growth and probably the production of secondary defense metabolites. Defense through volatile compounds was not induced by the aphid, and even suppressed in some cases, but the reasons behind this phenomenon remain to be elucidated. The production of melezitose-rich honeydew will promote its consumption by foraging insects, including honeybees, compromising their health and the quality of honey-derived products. Unwanted insects (such as other invasive species—ants and *Vespula* wasps) and generalist predators can be also attracted to this nutrient-rich source, potentially endangering native species, and disrupting their ecological interactions. The deposition of honeydew on the soil will promote microorganism growth and activity, having cascading effects on soil properties and communities.

A possible management strategy is the replacement of willows for native species or resistant willow clones, but this may not be always feasible due to high costs involved and native species not being suitable for the same uses. The use of biocontrol agents, in particular the specialized parasitoid *Pauesia nigrovaria,* seems to be a promising avenue to manage the aphid. The use of chemical controls is not possible at a large scale due to its negative impacts on bees and native insects and is only recommended in localized urban areas where other pests (such as wasps) are a threat to human health.

Although this work represents a comprehensive study on the multiple impacts of an invasive phytophagous insect, many aspects were not quantified and the mechanisms behind some of the observed patterns remain unclear. Therefore, we encourage further research on this system. It is also important to highlight that this study was conducted over a 2-yr period, so the long-term effects of the aphid attack and honeydew deposition on host plants, surrounding communities and the environment remain unknown.

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