Can international experience help us to predict the potential impacts of willow sawfly (*Nematus oligospilus* Förster) on willow populations in Australia?

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Abstract

In riparian areas and wetlands of south eastern Australia, willows (*Salix* spp.) are a serious weed. The recent arrival of willow sawfly (*Nematus oligospilus*) has the potential to affect willow management activities as the larval stage of the insect can cause whole tree defoliation and eventually tree death. Willow sawfly is native to the Holarctic region of the Northern Hemisphere but since 1980 has become an important invasive species in South America, southern Africa and New Zealand. Willow sawfly is capable of completing up to six generations per season in its invasive range, with population levels affected by temperature, climate (possibly conditions in early spring) and natural enemies. Tree willows tend to be more highly preferred by willow sawfly than shrub willows. Severe defoliation has so far been observed on nine *Salix* taxa in Australia, however there have been no reports to date of willow sawfly causing the death of entire willow trees. If the activity of willow sawfly does result in high levels of tree death across much of the landscape, then the implications for willow management include the possible redirection of resources from tree willows to shrub willows, and the development of techniques to establish native riparian vegetation in areas currently dominated by willows. It is too early to determine if populations of willow sawfly will affect willow populations and their management in Australia.

Keywords: native riparian vegetation, *Nematus oligospilus*, *Salix*, willow, willow sawfly.

Introduction

In much of south-eastern Australia, willows (*Salix* spp.) are serious weeds of waterways and wetlands, due to their highly invasive nature and detrimental impacts on river health. These impacts include modification of stream channels and hence river flows, exacerbation of riverbank erosion, exclusion of native species from riparian vegetation communities, increased allochthonous input seasonally, alteration of in-stream food webs and reduction of access for recreational pursuits (Cremer 2003). Due to their ability to reproduce both sexually and vegetatively, particularly via stem fragments, many willow species which were deliberately introduced for a range of purposes have become naturalized (Bruzzese and McFadyen 2006). The weedy potential of the genus led to the listing of all *Salix* taxa except *S. babylonica*, *S. × calodendron* and *S. × reichardtii* as Weeds of National Significance in 1999 (ARMCANZ *et al*. 2001).

Significant resources are invested in willow management by both public and private land managers, particularly Natural Resource Management agencies. Extensive willow control programs are undertaken annually in many catchments, targeting particular willow taxa or areas with high value natural or productive assets. In Victoria alone, approximately $A10m is spent on willow management programs each year (S. Holland Clift personal communication). The majority of these programs seek to control willows as part of the process of restoring native riparian vegetation communities, so replanting of native species usually follows willow control.

Willow management activities involve either physical or chemical control options, or a mixture of physical and chemical options (Holland Clift and Davies 2007). Biological control agents are not currently available, so the recent discovery of willow sawfly, *Nematus oligospilus* Förster (Hymenoptera: Tenthredinidae), in Australia is of great interest to willow managers. The larval stage of willow sawfly feeds almost exclusively on willow leaves and where high populations of willow sawfly develop, entire trees are defoliated. Although affected trees can regrow new leaves following defoliation, these leaves are often consumed by a new generation of larvae and so trees may be defoliated repeatedly over the growing season.

This paper reviews the existing literature on willow sawfly, with particular reference to the factors which affect willow sawfly populations, the impact of willow sawfly on willows in its invasive range (the Southern Hemisphere) and the taxa preferences of the insect. The paper aims to analyse this information in order to predict the likely impact of willow sawfly on willow populations and their management in the Australian landscape.

Worldwide distribution of willow sawfly

Native to the Northern Hemisphere, *N. oligospilus* is widespread in the Holarctic (northern) Region of Europe (Koch and Smith 2000). It is also found in Eurasia and in North America from Alaska to Mexico (Bruzzese and McFadyen 2006). Despite this considerable home range, Carr *et al*. (1998) considered that the dispersal capability of the insect was low on a local scale, but this has not proved to be the case in the Southern Hemisphere.

Nematus oligospilus was first recorded in the Southern Hemisphere in Argentina in 1980/81 (Dapoto and Giganti 1994), and was initially described as a new species (*Nematus desantisi* Smith 1983). However, Koch and Smith (2000) later identified it as the previously described Northern Hemisphere species *N. oligospilus.* Willow sawfly spread quickly and was detected in Santiago, Chile in 1983/84 (Dapoto and Giganti 1994). The insect was then found in Lesotho in southern Africa in October 1993 following the severe defoliation of willow trees, although the extent of defoliation suggested that willow sawfly was probably present in the area the previous summer (Urban and Eardley 1995).

The next report of *N. oligospilus* in the Southern Hemisphere was from Auckland, New Zealand, in February 1997 (Berry 1997). A survey undertaken in late summer 1997 found that willow sawfly was present throughout urban Auckland and it was also reported in Rotorua, about 230 km south of Auckland (van Kraayenoord 1997). The extent and severity of these infestations indicate that willow sawfly had been present in New Zealand for some time, perhaps two years or more, before being noticed (Berry 1997, van Kraayenoord 1997).

The first confirmed sighting of *N. oligospilus* in Australia occurred in Canberra, Australian Capital Territory (ACT), in March 2004 (Bruzzese and McFadyen 2006). Since this first report, willow sawfly has been found across much of south-eastern Australia, including Tasmania (Ede 2006, Finlay and Adair 2006, Ede *et al*. 2007). Areas where population numbers are high enough to cause severe tree defoliation include the Adelaide Hills, South Australia; central and southern New South Wales (NSW); the ACT; and north-eastern, central and southern Victoria (Ede *et al*. 2007). The population dynamics of willow sawfly indicate that it is likely that the insect was present in low numbers in Australia undetected prior to 2004.

It is unclear how willow sawfly has dispersed initially from its native range to the

Southern Hemisphere, and then between the continents and islands of the Southern Hemisphere. There is no evidence that deliberate introductions of willow sawfly were made into any of these countries. Urban and Eardley (1997) believe that the most likely route of introduction into southern Africa was via cocoons on illegally imported willow material. It is possible that from there, willow sawfly arrived in New Zealand, as diapausing, cocooned larvae on shipping containers (Charles *et al*. 2004). The insect may have been similarly transported to Australia, from New Zealand, southern Africa or South America, or it is possible that adults were blown across the Tasman Sea from New Zealand by easterly winds (Bruzzese and McFadyen 2006).

Impacts of willow sawfly on willows

In its native range, willow sawfly appears to be a relatively insignificant herbivore having little impact on willows due to its low population density and the relatively limited consumption of willow leaves by the larvae (Carr *et al*. 1998). However as an invasive species, the insect has had significant detrimental impacts on willows at sites where population densities have been able to develop to very high levels. In Argentina, severe defoliations, repeated defoliation events and tree deaths have been reported in willows (Dapoto and Giganti 1994, Alderete and Liljesthröm 2004), while severe defoliation of willows has also occurred in Chile (Gonzalez *et al*. 1986). Repeated severe defoliation has resulted in extensive willow tree deaths in southern Africa (Urban and Eardley 1997) and in New Zealand (Charles *et al*. 2004, Cowie 2006).

In Australia, it is not yet possible to confirm whether any willow trees have been killed by willow sawfly, but in areas where trees have been severely defoliated for two or more seasons, there is evidence of substantial dieback. Up to 50% of branches have died in some trees monitored regularly in the Kiewa Valley in north-eastern Victoria, as a result of two seasons of severe defoliation (F.J. Ede unpublished data).

The immediate consequence of tree defoliation is most obviously the loss of photosynthetic ability which then impacts on other aspects of tree functioning. Pot trials in young willows artificially defoliated on a four weekly basis resulted in the loss of more than 90% of root biomass (I. McIvor personal communication) which corroborates observations of substantial root loss in mature trees defoliated in the field (G. Hansen personal communication). It is likely that trees affected by some degree of willow sawfly defoliation are more susceptible to other biological and environmental stressors, including pest and pathogen infestations, and drought.

Population dynamics

Populations of willow sawfly in the Northern Hemisphere include both males and females, with collections in Europe and Canada containing similar numbers of members of each sex (Koch and Smith 2000, V. Caron personal communication). However in the Southern Hemisphere, populations appear to be thelytokous i.e. consist entirely of females (Urban and Eardley 1995, Koch and Smith 2000), which reproduce by parthenogenesis. This reproductive strategy allows for the rapid development of populations as mating is not required.

At the beginning of the season (September – October in south-eastern Australia) adult willow sawflies emerge from over-wintering cocoons and immediately commence egg-laying. Eggs are laid singly. Studies of different willow sawfly populations have found varying levels of fecundity. In one population within its native range, adults laid between 29 and 35 eggs (Carr *et al.* 1998), while more than 60 eggs were laid on average per adult in populations in southern Africa (Urban and Eardley 1995) and Argentina (Ovruski 1994). Lower fecundity was found in other Argentinean populations (13–24 eggs per adult, Dapoto and Giganti 1994).

In favourable conditions willow sawfly can complete its life cycle within about four weeks, but development times do vary between populations, as the data in Table 1 illustrate.

Factors that influence population development

There appear to be a number of factors, both physical and biological, that influence the development of willow sawfly populations, as illustrated by the variation in generation times presented in Table 1.

Temperature

Charles and Allan (2000) investigated the effect of temperature on willow sawfly development by rearing cohorts of willow sawfly in the laboratory at a series of constant temperatures. They found that development periods for each life stage tended to decrease with increasing temperature, although no eggs survived at 28.8°C. The mean generation time decreased from 108 days for willow sawfly reared at 11.3°C to 22–23 days for those reared at 23°C, 26°C and 28.8°C. Extrapolation from these data showed that the lower development threshold was 8.1°C and that a total of 321 degree-days above this threshold are required to complete one generation of willow sawfly (Charles and Allan 2000).

Although generation times decreased with increasing temperature in these studies, optimum temperatures for willow sawfly development were between 15.5°C and 19°C. Within this temperature range, adult body length and potential fecundity were highest and the number of larvae requiring more than five instars was reduced (Charles and Allan 2000). It has been hypothesized that as willow sawfly is native to predominantly cooler regions of the Northern Hemisphere, it may be intolerant of the high temperatures that regularly occur in summer in south-eastern Australia (Ede 2006). However, results from regular monitoring of both willow sawfly populations and daily temperatures at sites in north-eastern Victoria in the 2006/07 season indicated that the high temperatures experienced in that season (including several daily maxima above 40°C) did not have an obvious detrimental impact on the development of willow sawfly populations (Ede *et al*. 2007).

Table 1. Duration (days) of life stages and number of generations per year for different willow sawfly populations.

Population location	Egg	Larva	Pupa	Adult	Generations per year	Reference
Argentina	6–7	21	4–8	3–7	4–5	Dapoto and Giganti (1994)
Arizona, USA	9–11	19–20	–[A]	–	–	Carr *et al.* (1998)
Chile	–	–	–	–	2	Gonzalez *et al.* (1986)
New Zealand (NZ)	–	–	–	3–13	–	Charles *et al.* (1998)
East Coast, North Island, NZ	–	–	–	–	5–6	Charles *et al.* (2004)
NZ: 19°C (lab)[B]	6	14	9	–	–	Charles and Allan (2000)
Southern Africa	6	14	9	–	4	Urban and Eardley (1995)

[A] Data not provided.
[B] This temperature was maintained constantly in a laboratory environment.

Climate

Alderete and Liljeström (2004) studied willow sawfly populations over several seasons in two river valleys in Argentina with contrasting climatic patterns. One valley has a humid-temperate climate and the other a sub-humid cold climate. Defoliation events were recorded in two different seasons in each river valley over the study period. However, there were no significant differences in mean temperature, mean maximum temperature or rainfall within each valley between those years in which willow sawfly populations built up to levels sufficient to cause tree defoliation and the years with low population levels and no defoliation.

Anecdotal evidence from field observations in New Zealand indicate that warm, dry spring conditions favour rapid development of willow sawfly populations and lead to tree defoliation early in the season (D. Gorst personal communication). As well, adult fecundity and adult size are greater, and generation times shorter, in spring than in summer or autumn in New Zealand (J. Charles personal communication). Thus under favourable spring conditions there is potential for willow sawfly populations to develop rapidly, as adults lay more eggs and generation times are short. There are insufficient data from studies in Australia to verify these observations at this stage.

Natural enemies

It is likely that several species of parasites and predators act as natural enemies on populations of *N. oligospilus* in its home range. Three species of Hymenoptera have been reported as parasitoids associated with willow sawfly in California, USA (Alderete and Fidalgo 2004). Carr *et al*. (1998) reported variable levels of parasitism on willow sawfly eggs in different willow populations in Arizona, USA, with more than 80% of eggs parasitized at one site. The parasitoid species were not identified.

In Southern Hemisphere populations of willow sawfly, a limited number of parasitic and predatory species have been described, all of which are either Hymenoptera or Hemiptera (Gonzalez *et al*. 1986, Dapoto and Giganti 1994, Urban and Eardley 1995, Berry 1997, Alderete and Liljeström 2004). Urban and Eardley (1997) considered that the parasitic wasp *Dibrachys cavus* Walker (Hymenoptera: Pteromalidae) was introduced with willow sawfly, as it was previously unknown in southern Africa. Although populations of willow sawfly were initially sufficient to defoliate and kill willows in parts of southern Africa (Urban and Eardley 1997), the insect has now virtually disappeared, probably due to the activities of natural enemies (C. Eardley personal communication).

In Argentina, the exclusion of natural enemies led to a significant increase in survivorship of willow sawfly larvae (Alderete and Liljeström 2004). Larval mortality was found to be density-dependent and the impact of natural enemies (including *D. cavus*) was believed to be sufficient to regulate the willow sawfly population.

There have been no reports of natural enemies affecting willow sawfly populations in Australia yet. There are only three native species of Tenthredinidae in Australia (Naumann *et al*. 2002), so it is unlikely that there are many specific willow sawfly predators or parasites in the native Australian invertebrate fauna. It is unknown if generalist native species will significantly impact on willow sawfly populations (Bruzzese and McFadyen 2006).

Preferred taxa

Observational and experimental evidence from both Australia and overseas suggests tree willows (*Salix* subgenus *Salix*) are more susceptible to willow sawfly than shrub willows (*Salix* subgenus *Vetrix*), and that in some localities upright tree willows may be preferred over weeping taxa.

Willow sawfly has been observed on several willow taxa (listed in Table 2) in numerous locations across south-eastern Australia. Significant levels of defoliation, including whole tree defoliation, have been reported for many of the tree willow taxa (Table 2). Of the shrub willows, whole plant defoliation has only been observed on *S. purpurea* (purple osier) (D. Clements personal communication). This species was also found to be susceptible to willow sawfly in New Zealand (G. Hansen personal communication).

Although willow sawfly has been found on the shrub willows *S. cinerea* and *S.* × *reichardtii* (Table 2), most populations of willow sawfly on these species are low and have caused limited damage to isolated leaves (Finlay and Adair 2006, Ede *et al.* 2007). However a modest willow sawfly population has developed on *S. cinerea* at one site in north-east Victoria, with several larvae observed and a small number of leaves almost entirely consumed by willow sawfly (Ede *et al.* 2007). Ongoing monitoring of this site will determine whether this population can develop on *S. cinerea* to the extent required to cause extensive defoliation of the host plants.

In addition to those taxa listed in Table 2, willow sawfly has been observed to defoliate other willow taxa in other countries. In Argentina, Dapoto and Giganti (1994) reported defoliation of *S. elegantissima* (Thurlow weeping willow) and *S. alba* (white willow), while Koch and Smith (2000) noted the presence of willow sawfly on *S. caprea* (goat willow) and *S.* 'Erythroflexuosa' (golden tortured willow). In New Zealand, the shrub willows *S. elaeagnos* × *daphnoides* 'Tiritea' (hoary × violet willow) and *S. repens* × *purpurea* 'Kumeti' (creeping willow × purple osier) are considered to be susceptible to defoliation by willow sawfly (Ede 2006).

Table 2. Records of willow sawfly presence and of severe defoliation caused by willow sawfly on various willow taxa (*Salix*) in Australia.

Willow taxa	Common name	Willow sawfly present	Severe defoliation
Tree willows: *Salix* subgenus *Salix*			
S. fragilis	crack willow	Yes[A,B]	Yes[B]
S. × *rubens*	crack × golden hybrid	Yes[A,B]	Yes[B]
S. alba var. *vitellina*	golden willow	Yes[A,B]	Yes[B]
S. humboldtiana	Chilean pencil willow	Yes[A,B]	Yes[B]
S. nigra	black willow	Yes[B]	Yes[B]
S. alba × *matsudana*	New Zealand hybrid willow	Yes[A,B]	No
S. matsudana 'Tortuosa'	tortured willow	Yes[A,B]	Yes[B]
S. babylonica	weeping willow	Yes[A,B]	Yes[B]
S. × *sepulcralis* var. *sepulcralis*	weeping willow	Yes[A]	No
S. × *sepulcralis* var. *chrysocoma*	golden weeping willow	Yes[A,B]	Yes[B]
Shrub willows: *Salix* subgenus *Vetrix*			
S. cinerea	grey sallow	Yes[A,B]	No
S. × *reichardtii*	pussy willow	Yes[B]	No
S. purpurea	purple osier	Yes[B]	Yes[C]
S. viminalis	osier	No[A]	No

[A] Finlay and Adair 2006.
[B] Ede *et al*. 2007.
[C] D. Clements personal communication.

In laboratory trials in New Zealand with a range of willow species and hybrids, willow sawfly oviposited on tree willows in preference to shrub willows, with the exception of *S. purpurea* which was selected for oviposition at similar rates to the tree willows (Charles *et al*. 1998). Feeding trials with more than 20 willow taxa, including both shrub and tree willows, found that willow sawfly would feed on all species under study, but that the rates of larval development differed depending on the willow species being consumed. Larvae developed most rapidly on *S. alba*, while their least rapid development occurred while feeding on *S. babylonica* (J. Charles personal communication). These laboratory trials indicate that willow sawfly has the potential to oviposit and feed on a wide range of willow taxa, but this does not necessarily mean that willow sawfly will establish and flourish on all taxa in the field.

Poplars (*Populus* spp.) are the only other species on which willow sawfly has been observed in the field. In Argentina, Dapoto and Giganti (1994) considered both *P. alba* (white poplar) and *P.* × *canadensis* (Canadian poplar) as hosts of willow sawfly, and Koch and Smith (2000) also noted *P. nigra* (black poplar) as a host. In Hawkes Bay in New Zealand, some defoliation of poplars has been observed when larval numbers are so high that nearby willows have been completely defoliated and larvae are searching for alternative food sources (G. Hansen personal communication).

Laboratory feeding trials with early instar larvae on two poplar clones in New Zealand showed that larvae could complete development on these plants (J. Charles personal communication). In contrast, Urban and Eardley (1995) reported from glasshouse trials in South Africa that generally willow sawfly larvae did not survive on leaves of *P. deltoides* (matchstick poplar, eastern cottonwood), indicating that although occasional larvae are found on poplars in the field, there is little threat to poplars from willow sawfly in southern Africa.

In Australia there have been limited reports of willow sawfly on poplars, with occasional eggs and adults found on Lombardy poplars (*P. nigra* 'Italica') in north-east Victoria in the 2006/07 season (Ede *et al*. 2007). No willow sawfly larvae were observed on these trees. In February 2008, larvae were found on Lombardy poplars in southern NSW, at sites in the Bathurst region where the surrounding willows had been completely defoliated by willow sawfly (T. Hunt personal communication). In April 2008 at a site in north-east Victoria with a high willow sawfly population, larvae were observed on the leaves of poplar suckers and had caused some leaf damage (personal observations).

There are no reports of *N. oligospilus* being found on any taxa other than *Salix* and *Populus*, and there have been no observations of willow sawfly appearing on any native species in New Zealand (I. McIvor personal communication). It is highly unlikely that the *N. oligospilus* will attack any taxa other than willows and poplars in Australia, but further study is underway to test this assumption.

Patterns and predictions

For those land managers seeking to manage willow populations in their catchments in south-eastern Australia, the key questions posed by the arrival of willow sawfly relate to whether or not the insect will kill willows or significantly impact on their management activities. Overseas experience has shown that repeated, severe defoliation events can kill willow trees in other Southern Hemisphere countries (Dapoto and Giganti 1994, Urban and Eardley 1997, Alderete and Liljesthröm 2004, Charles *et al*. 2004, Cowie 2006), so although it is not yet possible to attribute the death of any willows in Australia to the activity of willow sawfly, it is highly likely that willow tree deaths will occur as a consequence of repeated defoliation by willow sawfly.

It is unclear how much time is required for willow sawfly populations to increase from very low numbers to levels sufficient to cause defoliation, either in Australia or elsewhere. Reports of willow sawfly generally relate to defoliation events, and there is limited monitoring of sites prior to this stage. A current research project monitoring willow sawfly populations in Victoria includes sites from which willow sawfly was either absent at the commencement of monitoring or present in very low numbers (Ede *et al*. 2007). Ongoing assessment of these sites will provide land managers with some indication of how many seasons elapse between the arrival of willow sawfly at a site and the development of population levels sufficient to cause tree defoliation, and subsequent tree death.

It is also difficult to conclude from the available evidence whether or not high populations of willow sawfly will be sustained over time. To date, defoliation of willows by willow sawfly has occurred in some parts of south-eastern Australia since 2004 and there are no signs of decline in willow sawfly populations at most sites. At one site in north-east Victoria however, golden willow trees (*S. alba* var. *vitellina*) were defoliated by willow sawfly during the 2005/06 season, but in the 2006/07 and 2007/08 seasons, willow sawfly populations were low and caused no significant tree defoliation (F.J. Ede, unpublished data). The reasons for the decline in the willow sawfly population at this site are unknown.

In New Zealand, outbreaks of willow sawfly initially caused widespread defoliation of willow trees in several regions in the North Island, with tree deaths occurring at many sites (Cowie 2006). However, high populations were not sustained in most regions for more than two or three years, with the exception of Hawke's Bay in the lower eastern coast of the North Island. Willow sawfly was first noticed in this region in 1999 with severe defoliation events occurring in the following five seasons (G. Hansen personal communication). Population levels have been lower in the past two seasons with little impact observed on willows throughout the region, and this has been at least partly attributed to cool, wet weather during spring (D. Gorst personal communication).

There has also been a significant decline in willow sawfly populations in southern Africa from levels that were initially high enough to defoliate willow trees, which is probably a consequence of the activity of natural enemies (C. Eardley personal communication). It is possible that in Australia, the development of willow sawfly populations will follow this boom and bust pattern, becoming limited by either biological or environmental factors, and that in years to come willow sawfly may not pose any threat to willow populations. However, there is currently insufficient evidence to predict either the likelihood of this outcome or the time frame of its occurrence.

What is more readily apparent from both overseas experience and Australian observations is that willow sawfly has a marked preference for tree willows over shrub willows, with only limited exceptions. This has potential implications for willow management activities as it may provide the opportunity to shift the investment focus of willow management programs from species of trees willows to shrub willows, if large areas of tree willows are adversely affected by willow sawfly (Ede 2007).

It is also possible that in sites where active willow control is a low priority, that defoliation by willow sawfly could assist with the re-establishment of native riparian species. Under intact willow canopies, very low light levels (Ede *et al.* 2007) make it difficult for native plants to establish. However, defoliation by willow sawfly significantly increases light to the understorey. By under-planting willows defoliated by willow sawfly with tube stock or augmenting the seed-bank through direct seeding, it may be possible to establish a healthy riparian community dominated by native species without the requirement to invest in willow removal (Ede 2007).

The presence of high populations of willow sawfly and subsequent tree defoliation is likely to affect the efficacy of willow control techniques at sites where foliar spraying or stem injection techniques are the preferred management options, as the limited leaf canopy will affect uptake and translocation of the applied herbicide.

The impact of willow sawfly on willows in several other countries where it is an invasive species does provide some answers to questions arising about its likely impacts in Australia. When willow sawfly population levels are high, tree defoliation occurs and repeated tree defoliation can lead to tree death. However, the paucity of data relating to both environmental and biological controls on population growth makes it difficult to determine whether or not willow sawfly will have a significant impact on willow populations and their management in Australia in the longer term.

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