



The Asian chestnut gall wasp *Dryocosmus kuriphilus*: a global invader and a successful case of classical biological control

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Abstract

Native to China, the Asian chestnut gall wasp, *Dryocosmus kuriphilus* (ACGW), was first found outside its native range in Japan and the Korean peninsula in the mid-twentieth century. After appearing in North America in 1974, it was found in Europe a few decades later. Since then, the gall wasp has spread throughout the distribution of chestnut in Europe. The ACGW's discovery in North America and Europe elicited numerous studies to understand its invasive potential in these areas and how to control its spread and impact on chestnut production. Although endemic parasitoids responded positively to *D. kuriphilus* with low parasitism rates, the most effective management tactic has been classical biological control via the introduction of the parasitoid *Torymus sinensis* from its native range in China. This review summarizes the history of introduction, spread, and current distribution of *D. kuriphilus*, and highlights one of the most successful cases of classical biological control against a forest pest.

Keywords *Dryocosmus kuriphilus* · Asian chestnut gall wasp · *Torymus sinensis* · Biological control · Invasive pest

Key message

- The Asian chestnut gall wasp, *Dryocosmus kuriphilus*, is one of the most successful invasive pest species worldwide, and since the mid-twentieth century, it has become established in Japan, North America, and Europe.
- The rapid and successful invasion history of *D. kuriphilus* is due to its parthenogenetic reproduction, lack of

effective natural enemies in its new ranges, and most importantly, human-mediated transport of infested plant material.

- Classical biological control via the introduction of *Torymus sinensis* seems to be the most effective control method of *D. kuriphilus*, and populations of this parasitoid are established in Japan, North America, and Europe.

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Introduction

Invasive species are important disturbance factors in natural and managed systems worldwide (Liebhold et al. 2017), directly and indirectly affecting many ecosystem processes (Crowl et al. 2008; Kenis et al. 2009), significantly impacting the global economy (Pimentel et al. 2001; Paine et al. 2016), and increasingly dominating the field of forest entomology (Holmes et al. 2009; Brockerhoff and Liebhold 2017; Meurisse et al. 2018). For instance, the emerald ash borer, *Agrilus planipennis* Fairmaire (Coleoptera, Buprestidae), native to China, has established in North America (Herms and McCullough 2014) and European Russia (Orlova-Bienkowskaja 2014) and has likely contributed to the loss of millions of trees in urban and rural landscapes.

It also costs public and private entities billions of dollars in damage (Aukema et al. 2011). In Europe, numerous introduced alien insect species have established (Hulme et al. 2009) and expanded to neighboring countries via natural dispersal and human-assisted transport (Roques et al. 2016; Meurisse et al. 2018).

Hymenoptera are one of the most abundant orders among invasive insects (Roques 2010; Matošević and Pajač 2013; Avtzis et al. 2017) in part because their minute size and cryptic life histories make them difficult to detect (Roques 2010). The Asian chestnut gall wasp (ACGW), *D. kuriphilus* Yasumatsu (Hymenoptera, Cynipidae), is one of a long list of invasive alien hymenoptera to establish outside its native range. Its rapid expansion capabilities, coupled with its associated ecological and economic damage, make the ACGW one of the most important pests of chestnuts (*Castanea* spp.) worldwide (EFSA 2010). In Europe, ACGW has devastated chestnut production with yield losses up to 80% (Battisti et al. 2014) and has contributed to reductions in chestnut wood growth (Gehring et al. 2018), and an overall decline in chestnut tree health (EFSA 2010). Yet as dire as the situation may be, biological control efforts for the ACGW have been rather successful using a parasitoid from its native range. Here, we review the status of ACGW worldwide and highlight biological control programs in different countries.

Taxonomy and life history

About 1300 gall-forming wasp species (Cynipini) have been recorded globally (Csóka et al. 2004) and the vast majority infest *Quercus* spp. (Stone et al. 2002). ACGW is an exception, developing instead on *Castanea crenata* Siebold and Zucc., *Castanea dentata* (Marsh.) Borkh., *Castanea mollissima* Blume, *Castanea sativa* Mill., and their hybrids in the Palearctic region (Ács et al. 2007; Csóka et al. 2017). Another exception is the recently described *Dryocosmus zhuili* Liu et Zhu that induces leaf galls on *Castanea henryi* Skan in southeastern China (Zhu et al. 2015). While it is impossible to distinguish *D. zhuili* galls from those caused by the ACGW, Zhu et al. (2015) gave seven diagnostic characters to differentiate adult *D. zhuili* from ACGW. The species have similar phenology, and characteristics mentioned for *D. zhuili* females can also be found in European populations of the ACGW (Pérez et al. 2018). Zhu et al. (2015) reported a 2% genetic distance between ACGW and *D. zhuili*, which is not enough to determine if *D. zhuili* is a distinct species from ACGW (Hebert et al. 2003; Nicholls et al. 2012). Genetic distances between other *Dryocosmus* species are around 4.1–6.3% (Cerasa et al. 2018).

Unlike the majority of Cynipini, which have alternate sexual and asexual generations annually (Csóka et al. 2004; Abe

et al. 2007), ACGW is purely asexual (thelytokous) and univoltine (Otake et al. 1982). ACGW is highly synchronized with chestnut phenology (Bernardo et al. 2013). Females lay eggs in the buds of *Castanea* spp. during summer (June, July). Eggs hatch in 30–40 days and first instar larvae overwinter inside the buds. Larvae commence feeding when buds open the following spring, inducing the formation of galls inside which larvae develop and feed until adult emergence (Cho and Lee 1963). After adult emergence, lignified woody galls often persist on branches for several years (Brussino et al. 2002).

Invasion history

The long list of areas invaded by ACGW, including 25 countries in Asia, Europe, and North America, and particularly in the last 20 years (Table 1), demonstrates the invasive potential of this pest. Its rapid expansion is a consequence of unimpeded movement of infested plant material and of natural dispersal (Graziosi and Santi 2008). The continuity of chestnut stands in certain areas (e.g., Europe) also increases the risk and rate of infesting new areas.

ACGW is thought to have been introduced from China to neighboring Japan via infested plant material (Shiraga 1951). This pest demonstrated its damage potential as the lack of natural enemies (Yasumatsu 1951) enabled its populations to quickly reach outbreak levels (Oho and Shimura 1970). ACGW was later introduced to the southern USA on infested plant material (Rieske 2007). ACGW has continued to spread northward in the eastern USA and has been recorded in 12 states. It reached Canada in 2012 and is now confirmed in the Great Lakes Region (Haack 2015; Lizotte 2015). While some areas experience new infestations of invasive species through the natural movement of organisms, many new invasive species records are a direct result of human-mediated plant movement (Meurisse et al. 2018). For instance, it is unclear whether the ACGW arrived in Canada through natural range expansion or human-mediated introductions (Huber and Read 2012).

In Europe, ACGW was first reported in 2002 in Northwest Italy (Brussino et al. 2002) but, based on customs records, was likely introduced 2–3 years earlier with the importation of plant material from China (Quacchia et al. 2008). The European Plant Protection Organization (EPPO) added ACGW to its A2 Action List in 2003 (EPPO 2005). The speed of dispersal at the local population level is estimated (using a stratified dispersal model), to be less than 7 km/year (Gilioli et al. 2013), and long-term dispersal is solely human assisted, primarily with trade of infested planting material (Graziosi and Santi 2008; EFSA 2010). The strong invasive potential of the pest is enabled by a parthenogenetic reproductive strategy (Avtzis and Matošević 2013) and by adult

Table 1 Invasion history of the Asian chestnut gall wasp, *D. kuriphilus*

Country	Year found	References
Japan	1941	Shirakami (1951)
Korea	1958	Tamura (1962)
USA	1974	Payne et al. (1975)
Nepal	1999	Ueno (2006)
Italy	2002	Brussino et al. (2002)
France	2005	Aebi et al. (2006)
Slovenia	2005	Seljak (2006)
Switzerland	2007	Forster et al. (2009)
Hungary	2009	Csóka et al. (2009)
Croatia	2010	Matošević et al. (2010)
Netherlands	2010	EPPO global database: https://gd.eppo.int/taxon/DRYCKU/reporting
Canada	2012	Huber and Read (2012)
Czech Republic	2012	EPPO global database: https://gd.eppo.int/taxon/DRYCKU/reporting
Germany	2012	EPPO global database: https://gd.eppo.int/taxon/DRYCKU/reporting
Spain	2012	Pujade-Villar et al. (2013)
Austria	2013	EPPO global database: https://gd.eppo.int/taxon/DRYCKU/reporting
Greece	2014	Michaelakis et al. (2016)
Portugal	2014	EPPO global database: https://gd.eppo.int/taxon/DRYCKU/reporting
Romania	2014	Radócz et al. (2016)
Slovakia	2014	Pástor et al. (2017)
Turkey	2014	Çetğn et al. (2014)
Belgium	2015	EPPO global database: https://gd.eppo.int/taxon/DRYCKU/reporting
Bosnia and Herzegovina	2015	Delalić (2016)
Great Britain	2015	EPPO global database: https://gd.eppo.int/taxon/DRYCKU/reporting
Russia	2016	Gninenko and Lyanguzov (2017)

This insect was first observed in China in 1929 (Murakami et al. 1980) and determined to be native to that area

reabsorption of eggs when suitable hosts are not present, thus reallocating resources internally, increasing fitness, and potentially increasing invasive potential (Graziosi and Rieske 2014).

Impact

ACGW infestations indirectly reduce chestnut production by preventing the formation of female flowers and causing flower abortion (Conedera and Gehring 2015). Fruit yield can be reduced up to 80% (Battisti et al. 2014). ACGW damage results in branches with lower leaf area than unaffected branches, earlier leaf mortality and abscission, lower leaf biomass, and a reduced ability to produce winter buds (Kato and Hijii 1997; Sartor et al. 2015). ACGW damage can negatively affect CO₂ assimilation and stomatal conductance and lead to reduced photosynthesizing leaf surface area (Ugolini et al. 2014; Sartor et al. 2015). Massive attacks, more common in chronically infested areas, can constrain bud development and reduce shoot vigor (Ugolini et al. 2014). All these damages gradually lead to a reduction in tree vigor

(Kato and Hijii 1997; Ugolini et al. 2014; Sartor et al. 2015). Repeated yearly ACGW attacks result in severely malformed branch architectures including a decrease in dormant buds and an increase in dead shoots with leaf area losses of up to 70% (Gehring et al. 2018). Successive severe infestations combined with abiotic (e.g., drought) and/or biotic (e.g., fungal infection) tree stress factors may lead to mortality of younger trees (Moriya et al. 2003) which is of special concern in Mediterranean sweet chestnut forests that are under other environmental stress factors (e.g., changes in climate conditions, summer droughts) (Lieutier and Payne 2016).

An increase in *Cryphonectria parasitica* (Murill) Barr, an invasive and virulent fungal agent also known as chestnut blight, has been recorded in sweet chestnut stands infested with ACGW (Prospero and Forster 2011). Meyer et al. (2015) showed an indirect interaction between two highly invasive and damaging pests on the European chestnut in which dead or dying gall tissue was colonized by virulent strains of *C. parasitica* and served as an entry point of the fungus. This may reactivate the virulent strain in the stands where the disease is under control by hypovirulent fungal strains (Meyer et al. 2015).

In addition, the spread of ACGW may have increased the diffusion of a nut rot of chestnut caused by *Gnomoniopsis castaneae* Tamietti in the invaded area (Lione et al. 2016) and several other genera of fungi (mainly Ascomycetes) have been known to colonize abandoned ACGW galls, forming a new ecological niche of fungi associated with European sweet chestnut (Meyer et al. 2015).

Management

Within its native range in China, ACGW populations are regulated by a complex of natural enemies, including eleven species from five chalcid (Chalcidoidea) families (Murakami et al. 1980; Kamijo 1981). Early attempts to limit the impact of ACGW in Japan focused on the use of resistant chestnut varieties, which was initially very effective (Kajiura and Machida 1961). However, an adapted biotype of the wasp, capable of attacking resistant varieties, proliferated and rapidly took over (Shimura 1972), forming galls on trees initially described as resistant (Shimura 1973). In Europe, despite unsuccessful attempts to detect natural resistance (Brussino et al. 2002), the hybrid *C. crenata* × *C. sativa*, “Bouche de Betizac,” was found to be resistant to ACGW and is now used by growers (Dini et al. 2012). Recently, the red salernitan ecotype of *C. sativa* from southern Italy was shown to be moderately resistant to ACGW (Nugnes et al. 2018).

Shortly after its introduction and establishment in Italy, numerous attempts were made to control populations of ACGW, ranging from agrotechnical measures (e.g., pruning and burning of infested shoots, nursing propagation material in glass houses) to the application of conventional chemical insecticides in spring and at the beginning and end of summer (EFSA 2010). The use of insecticides against ACGW has proven to be ineffective as larvae are well protected in galls and not impacted by contact insecticides, while applications have to be perfectly timed to kill adults during their activity period (Bosio et al. 2010).

Pruning and disposal of infected branches may be an effective management method when very few trees are infected (Payne and Johnson 1979), but results in some loss of nut crop and would need to be repeated in subsequent years. This method is labor-intensive and economically unfeasible for large commercial growers (Payne et al. 1983).

Classical biological control, an effective method for controlling invasive species (Hajek et al. 2016), was explored for ACGW, considering natural enemies from the pest’s native and invaded ranges. In Japan, 24 species of endemic parasitoids were recorded on ACGW (Yasumatsu and Kamijo 1979; Kamijo 1981), whereas in the USA eight endemic parasitoid species have shifted onto the novel host (Rieske 2014). In Europe, populations of endemic oak gall wasps

are regulated by at least 104 species of chalcid parasitoids (Askew et al. 2013), most of which are generalists (Aebi et al. 2006, 2007; Schönrogge et al. 2006). Since 2012, 44 different chalcid parasitoid species belonging to six families (Eurytomidae, Pteromalidae, Torymidae, Eupelmidae, Ormyridae, and Eulophidae) have been reared from ACGW galls (Quacchia et al. 2012; Matošević and Melika 2013; Kos et al. 2015). However, native European parasitoids do not maintain ACGW population densities below acceptable economic damage levels because none of the parasitoid species are specialized on ACGW (Santi and Maini 2011; Quacchia et al. 2012; Askew et al. 2013; Matošević and Melika 2013; Francati et al. 2015; Kos et al. 2015). Low parasitism levels (2–32%) are probably due to asynchronization of their emergence times with ACGW life cycle (Quacchia et al. 2012). As a consequence, parasitoids from the ACGW native range were surveyed for potential classical biological control agents (Hajek 2008).

In China, ACGW populations are regulated by a complex of 11 hymenopteran parasitoid species (Bailey et al. 2009; Zhang 2009), of which *T. sinensis* Kamijo (Hymenoptera, Torymidae) seemed the most promising because it is univoltine, highly host-specific, and phenologically adapted to the life cycle of the ACGW (Kamijo 1982; Moriya et al. 2003). Parasitoid adults emerge from withered galls, mate, and females oviposit an average of 70 eggs in the newly developed galls of ACGW in spring, in synchrony with budburst of sweet chestnut and the development of new galls (Quacchia et al. 2008). Females of *T. sinensis* locate the host with a combination of visual and olfactory stimuli from fresh galls and chestnut foliage that partly explains its specificity to ACGW (Graziosi and Rieske 2013). Eggs laid directly on the host larva rather than the gall chamber wall indicate an adaptation of ovipositor length to ACGW gall structure (Piao and Moriya 1999). The parasitoid larva feeds ectoparasitically before it pupates in late winter the following year (Ferracini et al. 2015a). In addition to its synchrony with and specificity to its host, *T. sinensis* exhibits several traits that render it a highly efficient biological agent against ACGW (Otake 1987; Schönrogge et al. 2006), including the ability to enter a prolonged diapause to survive during periods of low host availability (Ferracini et al. 2015b).

Because of its biological control potential, *T. sinensis* was selected and released in southwestern Japan in the late 1970s and early 1980s (Murakami et al. 1980; Otake et al. 1982). In the following years, populations grew exponentially and soon it became the most abundant and successful parasitoid of ACGW in Japan (Aebi et al. 2006), reducing ACGW damage to below the tolerable injury threshold of 30% production loss (Gyoutoku and Uemura 1985). A similar conclusion was reached soon after *T. sinensis*’ 1977 introduction to Georgia, USA (Payne 1978); the parasitoid’s range expanded together with its host and gradually became

the most abundant parasitoid of ACGW in the eastern USA (Cooper and Rieske 2007, 2011). The North American situation is unique in that most of the native chestnuts had been killed by the invasive chestnut blight fungus in the early 1900s, and commercial chestnut culture is still in its infancy compared to other parts of the world (Payne et al. 1983; Warmund 2011).

Italy was the first European country to control the spread of ACGW by importing *T. sinensis* infested galls from Japan in 2005 (Quacchia et al. 2008). France soon followed (2011) and parasitism rate increased a few years later (Borowiec et al. 2014). Releases of *T. sinensis* in Slovenia, Croatia, and Hungary started in 2014 (Matošević et al. 2015), but high levels of parasitism before and immediately following the first releases indicated the parasitoid was already established there and was assumed to have arrived from Italy via natural dispersal (Matošević et al. 2017a). In support of this assumption, *T. sinensis* was found parasitizing ACGW in Bosnia and Herzegovina (Matošević et al. 2017b) where no release program has yet been conducted.

Initial studies in northern Italy showed slow population dispersal (Bosio et al. 2013), but only 9 years after the releases of the parasitoid, ACGW infestation rates in northern Italy have significantly dropped (Ferracini et al. 2018), as have those in Slovenia, Croatia, Hungary (Matošević et al. 2017a, b), and France (Borowiec et al. 2018).

Populations of *T. sinensis* grow exponentially following introduction (Borowiec et al. 2018). This is a consequence of high colonizing efficiency (Borowiec et al. 2018), rapid dispersal aided by wind (Colombari and Battisti 2016a), intrinsic properties including behavioral adaptation to locate hosts and mates (Borowiec et al. 2018), lack of competition with native parasitoids (Colombari and Battisti 2016b), and high genetic diversity without a bottleneck-induced founder effect phenomenon (Matošević et al. 2015).

There were major concerns in Europe that the non-native *T. sinensis* might hybridize with native *Torymus* species or shift to parasitize non-target, native gall wasps. Hybridization of a biological control agent with native species is considered an environmental risk to non-target species (Gibbs et al. 2011). In Japan, *T. sinensis* and *T. beneficus* Yasumatsu and Kamijo have been successfully crossed in the laboratory and produced fertile hybrid females (Moriya et al. 1992), and up to 22% hybrid individuals have been detected in the field in Japan (Yara et al. 2010). The probability of hybridization with native European *Torymus* species (Hymenoptera: Torymiidae) was tested in mating experiments on *Torymus flavipes* (Walker), *Torymus auratus* (Muller), *Torymus affinis* (Fonscolombe), and *Torymus geranii* (Walker). No mate recognition and mating were recorded in laboratory experiments with these species (Quacchia et al. 2014). However, experiments with *Torymus* species reared from oak and chestnut galls in Switzerland and Italy found one possible

case of hybridization between *T. sinensis* and *T. cyaneus* Walker in a laboratory setting (Aebi et al. 2013); extensive field sampling has yet to document *T. sinensis* hybridization with native *Torymus* species (Ferracini et al. 2017).

Host specificity tests initially showed no oviposition of *T. sinensis* on galls of *Mikiola fagi* Hartig (Diptera; Cecidomyiidae), asexual generations of *Cynips quercusfolii* L. and *Andricus kollari* Hartig (Hymenoptera, Cynipidae) (Quacchia et al. 2008), but these trials were considered insufficient because of the limited range of alternative galls on different plant species (Gibbs et al. 2011). Additional tests were redesigned and performed on species with similar ecology, spatial and temporal attributes, accessibility, and availability of *T. sinensis* during the period of parasitization, following the suggestions of EFSA (2010). Despite a few brief oviposition attempts on *Andricus cydoniae* Giraud, *Biorhiza pallida* L., and *Dryocosmus cerriphilus* Giraud, no eggs were laid (Quacchia et al. 2014), confirming field observations that followed its introduction (Aebi et al. 2013). An even more recent post-release study of *T. sinensis* verified it had no effect on non-target host densities (Ferracini et al. 2017).

In summary, it is evident that despite the initial expansion of ACGW in Europe with associated losses in chestnut production, the situation has been reversed. As previously observed in Japan and North America the introduction and release of the highly specific and well-adapted Chinese parasitoid, *T. sinensis*, gradually reduced ACGW's economic impact. Chestnut production in Italy, the first European country to introduce *T. sinensis* for biocontrol, recovers at a steady pace with parasitism now exceeding 90% in Northern Italy (Colombari and Battisti 2016b), something also seen in other countries (e.g., Croatia, Slovenia, and Hungary; Matošević et al. 2017a). In Northern Italy 13 years after the first release of *T. sinensis*, there is no report of ACGW resurgence (Ferracini et al. 2018).

Future challenges

Early post-introduction studies including population dynamics (Borowiec et al. 2018) and assessing the impact of *T. sinensis* on native gall inducers (Ferracini et al. 2017) have shown that classical biological control of ACGW with *T. sinensis* is a highly efficient and cost-effective method of managing this invasive pest. However, in France, it was shown the introduction of *T. sinensis* followed a two-phase process: first, an exponential growth of *T. sinensis* populations without a significant decrease in *D. kuriphilus* populations, and secondly a general decrease in both *D. kuriphilus* and *T. sinensis* populations (Borowiec et al. 2018). Paparella et al. (2015) predicted density waves of both host and parasitoid over time, and there are some examples of recurrent ACGW infestation followed by peaks of *T. sinensis* populations

(Ferracini et al. 2018). It is therefore important to implement long-term post-release studies to closely follow host-parasitoid population dynamics and to assess potential interactions of *T. sinensis* with native parasitoids and non-target hosts.

In North America, the situation is entirely different from that in Asia and Europe. Chestnut blight made American chestnut functionally extinct, but efforts to reintroduce this iconic tree are showing great promise—so much that a hybridized chestnut cultivar could be used to restore chestnut to American forests (Powell 2014). These efforts may be negatively influenced by the presence of ACGW, and resistance screening will need to account for this invasive pest. Fortunately, *T. sinensis* is already established in the USA (Cooper and Rieske 2011) and along with several native parasitoids (Rieske 2014) may help control ACGW populations.

Author contributions

DNA, DM, GM and DRC contributed to parts that regard their field of expertise; DNA, DM and DRC contributed to the article preparation and writing.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflicts of interests.

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