Chapter 14
Gall Formers

Brett P. Hurley, Gudrun Dittrich-Schröder, and Caitlin R. Gevers

14.1 Introduction

Gall formers are among the most highly evolved herbivores. Several organisms induce gall formation including viruses, bacteria, mites and nematodes. Insects are one of the most dominant gall-forming groups, with estimates ranging from 21,000 to 211,000 species (Ciesla 2011). Within the insects, gall formers have evolved independently in the Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera and Thysanoptera. Galls are induced by the gall-forming insect, where specific metabolic interactions result in differentiation of the plant tissue and the consequent abnormal growths are referred to as galls. Through this manipulation of the plant's growth, the insect obtains food and shelter. Galls can vary greatly in size and shape, from pits or folds to the 'oak apples' of some cynipid species. Gall forming insects often display fascinating and complex biologies, including host alternation and cyclical parthenogenesis. However, the biology of many gall formers is poorly understood, in part because of their cryptic habit of living primarily within the gall.

Historically, gall formers of trees have often been reported as pests of little economic importance. However, this has changed with the introduction and spread of a number of invasive non-native gall forming species, some of which have become pests of serious economic importance. Thus, for some forestry tree species like eucalypts this group of insects has now become one of the most important groups of insect pests (Dittrich-Schröder et al. 2020). The importance of gall formers as pests of forestry trees will increase in the future with the increased movement of these insects around the world.

In this chapter, we discuss insect gall formers of forestry trees. We examine the natural history and ecology, as well as the evolution and diversity, of these fascinating

B. P. Hurley (✉) · G. Dittrich-Schröder · C. R. Gevers
Department of Zoology and Entomology, Forestry and Agricultural Biotechnology Institute (FABI), University of Pretoria, Pretoria, South Africa
e-mail: brett.hurley@fabi.up.ac.za

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insects. We provide a list of the gall forming insects associated with forestry trees and discuss management strategies, with a focus on the species most relevant to forestry. In addition, we use case studies to discuss three of the important gall forming species, to provide more specific details of the biology, spread and management of these insects.

14.2 Natural History and Ecology

As a group gall forming insects are polyphyletic and include a variety of orders and families, and consequently represent a very diverse range of life histories. As it is not possible to cover the details of all the different gall formers in this chapter, we focus on three key aspects related to their natural history and ecology; namely gall formation, reproductive strategies and the gall community.

14.2.1 Gall Formation

Insect-induced plant galls are the product of a highly specialised and unique type of insect-plant interaction. Most gall forming insects have a high fidelity to a specific host genus or even species, and thus do not attack an extensive range of host plants (Csóka et al. 2017). In addition, most gall forming insects only attack specific plant organs of their host, for example the flowers, fruits, buds, shoots or leaves, and these organs must be in the correct development or phenological stage. Gall shape is generally consistent within a species, but not between related taxa, and thus gall morphology can be used to assist species identification (Raman 2011). As opposed to the abnormal growths induced by fungi and bacteria, 90% of galls induced by insects show bilateral or radial symmetry (Raman 2007).

Plant galls are an incredible example of a modified natural structure caused by messages from a foreign organism. Initiation of a gall occurs when the plant is either exposed to an accessory gland secretion during oviposition (e.g. cynipids, sawflies and some beetles), or a salivary chemical from the feeding of first-instar larvae (e.g. cecidomyiids, coccids and aphids) (Rohfritsch 1992). Subsequently the exposed tissues no longer experience normal growth but, instead, the cells are physiologically modified through differentiation and hypertrophy (increase in cell size), resulting in formation of the inner-gall tissue and the outer gall tissue (cortical parenchyma) (Harper et al. 2004; Klein 2009). The growth stage of the gall consists mainly of hyperplasia (cell expansion), which allows the gall and the inner chamber to grow. Hyperplasia results in the formation of nutritive tissue that the larvae are able to manipulate into a suitable food source (Rohfritsch 1992; Harper et al. 2004; Klein 2009). The larva is then able to feed on the inner-gall tissue for the duration of its development, thereby decreasing the number of gall cell layers as the larva increases in size.

The gall reaches maturity once cell proliferation ceases. Major physiological and chemical changes in the gall tissues, such as when the flow of water and sap to the gall stops, results in gall dehiscence (Rohfritsch 1992). These changes are correlated with the development of the gall former and facilitate its exit from the gall. Although there is limited information on the communication between gall inducer and host plant, it has become evident that constant stimuli by the gall inducer is required to retain gall formation (Stone et al. 2002; Harper et al. 2004). If a natural enemy kills the gall inducer, gall development will cease.

14.2.2 Reproductive Strategies

Gall forming insects are present in several orders and families, and, not surprisingly, there are a range of reproductive strategies associated with these insects, from sexual reproduction to parthenogenesis, where males are either lacking or very scarce (see Case Study—*Leptocybe invasa*). Perhaps one of the most interesting reproductive strategies, present in a number of gall forming insects in the Hemiptera (Adelgidae and Pemphigidae) and Hymenoptera (Cynipidae), is that of cyclical parthenogenesis. Cyclical parthenogenesis involves the alternation of sexual and asexual reproduction. This reproductive mode has been described in over 15,000 species (Stone et al. 2008). The alternation of reproductive modes within a year is often associated with differences in morphology and ecology among generations. The differences between these generations can be so great that some gall formers were originally identified as different species and even genera (Felt 1940). In some cases, the different reproductive modes are associated with different host plants (see Case Studies—*Adelges cooleyi* and *Andricus* spp).

Oak and sycamore gall wasps (Cynipidae) are unique as they produce their asexual and sexual generations in strict alternation (Stone et al. 2002, 2008; Atkinson et al. 2003). This is unlike other gall wasps, which reproduce asexually with the occasional sexual generation in response to environmental changes. Many of the cynipids exhibit obligate alternating sexual and asexual generations (Hood and Ott 2011). These generations differ by the host plant used, the plant part galled, morphology and size of the gall, the number of siblings in each gall and the adult body size (Stone et al. 2002; Rokas et al. 2003; Stone and Schönrogge 2003; Hood and Ott 2011; Schönrogge et al. 2012). A common difference observed between sexual and asexual generations is that asexual galls are large and complex while the sexual galls are simple, often cryptic and usually much smaller.

14.2.3 Gall Community

Galls can contain multitrophic, closed and complex communities with a number of different inhabitants, including the gall inducer, parasitoids, hyperparasitoids, and inquilines (Table 14.1). Parasitoids may feed exclusively on the host gall former, but in some parasitoid species the larvae initially feed on the gall tissue and then switch to feed on the host, while in other species the larvae start by feeding on the host and later feed on the gall tissue in order to complete their development (Roskam 1992; Klein 2009). There is a great diversity of parasitoids of gall formers, and in some cases there are different cohorts of parasitoids of the sexual and asexual galls of the same species (Table 14.1).

Inquilines inhabit galls of other insects to obtain food and shelter. They are incapable of inducing galls of their own but, as with the parasitoids of gall insects, they are highly specialised to gain access to existing galls. Unlike parasitoids, however, inquilines do not feed on the developing gall insect but obtain their nutrition from the gall tissues (Brooks and Shorthouse 1998). The gall inducer and inquiline can sometimes co-exist and partition the gall resources, resulting in the successful development of both species. In other cases, the inquiline may cause the death of the gall inducer because it either develops and feeds much faster than the gall inducer, causing it to starve, or it manipulates the gall, creating additional chambers and tissues of its own (endohalls), which cause the gall inducer to die due to insufficient space or crushing (Brooks and Shorthouse 1998; Ferraz and Monteiro 2003; Klein 2009). Although some gall communities are relatively well studied, in many cases the taxonomy and role of the different gall inhabitants is not well resolved.

14.3 Evolution and Diversity

The ability to form galls has evolved many times in phytophagous insects and has been recorded from six insect orders (Cook and Gullan 2004; Hardy and Cook 2010). More than 13,000 insect species have been described as gall inducers (Raman et al. 2005); however, the two families with the greatest number of species are the Cecidomyiidae (Diptera) and Cynipidae (Hymenoptera), with each family comprising approximately 1400 described species (Dreger-Jauffret and Shorthouse 1992; Ronquist and Liljeblad 2001; Ronquist et al. 2015) (Fig. 14.1).

The complex relationship between the gall former and host plant is considered to be an advanced association (Shorthouse et al. 2005). Gall forming insects have been shown to be highly host and tissue specific, showing significant phenotypical specificity and are significantly more host-specific than closely related non gall-forming species (Hardy and Cook 2010). An example, illustrating the phenotypic specificity, are the cynipids associated with oak, which are represented by more than 1000 described species, with each species having a characteristic gall structure (Stone and Cook 1998; Ronquist and Liljeblad 2001). Evolution of gall formation is best-described using cynipids due to the extensive work conducted on this family. The ancestral origin of gall-forming cynipids is thought to be the Palearctic (Ronquist et al. 2015). Some of the oldest records of studies on the evolution of gall formation, date back to the 1920's. In these studies, Alfred Kinsey used morphological and biological information to explain the relationships between gall formers and their

Table 14.1 Examples of inquilines and parasitoids of gall insects that infest forest trees

Species	Inquilines	Parasitoids
Hymenoptera: Cynipidae		
Andricus burgundus	*Synophrus politus*	*Mesopolobus dubius, M. xanthocerus, M. mediterraneus, Ormocerus vernalis*, *Aulogymnus gallaru, A. testaceoviridis, Aprostocetus* sp. 1*, Tetrastichus* sp. 1*, Torymus auratus, Macroneura vesicularis*
Andricus corruptrix	Sexual generation: *Synergus reinhardii* & *S. umbraculus*	Sexual generation: *Mesopolobus dubius*, *M. fuscipes*, *M. tibialis* and *M. xanthocerus*
Andricus grossulariae	*Ceroptres cerri* (Cynipidae)	
Andricus kollari	Sexual generation: *Synergus reinhardii, S. umbraculus*	Sexual generation: *Mesopolobus dubius*, *M. fuscipes*, *M. tibialis* and *M. xanthocerus*
Andricus lignicola	Sexual generation: *Synergus reinhardii, S. umbraculus*	Sexual generation: *Mesopolobus dubius*, *M. fuscipes*, *M. tibialis* and *M. xanthocerus*
Andricus quercuscalisis (Knopper gall wasp)	Asexual galls: Synergus gallaepomiformis, S. umbraculus; Sexual galls: *Synergus reinhardii, S. umbraculus*	Asexual galls: *Sycophila biguttata, Mosopolobus amaenus*, *Megastigmus stigmatizana, Gelis formicarcius*. Sexual galls: *Mesopolobus dubius*, *M. fuscipes, M. tibialis* and *M. xanthocerus*
Dryocosmus kuriphilus (Chestnut gall wasp)		*Torymus sinensis*
Neuroterus saltatorius (Jumping oak gall wasp)		*Ormyrus distinctus*, *Amphidocius schickae*, *Mesopolobus longicausae*, *Dibrachys cavus*, *Amphidocius*n. sp., *Aprostocetus pattersonae*, *Aprostocetus verrucarii*, *Aprostocetus* n. sp., *Brasema* sp.
Hymenoptera: Eulophidae		
Leptocybe invasa (bluegum chalcid)		*Selitrichodes neseri*, *Quadrastichus mendeli, Selitrichodes kryceri*

(continued)

Table 14.1 (continued)

Species	Inquilines	Parasitoids
Ophelimus maskelli (eucalypt gall wasp)		*Closterocerus chamaeleon*
Quadrastichodella nova		*Leprosa milga*
Diptera: Cecidomyiidae		
Obolodiplosis robiniae		*Platygaster robiniae*
Thecodiplosis jaonensis (pine needle gall midge)		*Inostemma matsutama, I. seoulis*

References: Smith (1954), Claridge (1962), Hutchinson (1974), Payne (1978), Moriya et al. (1989b), Schönrogge et al. (1996), Walker et al. (2002), Ciesla (2011), and Schönrogge et al. (2012)

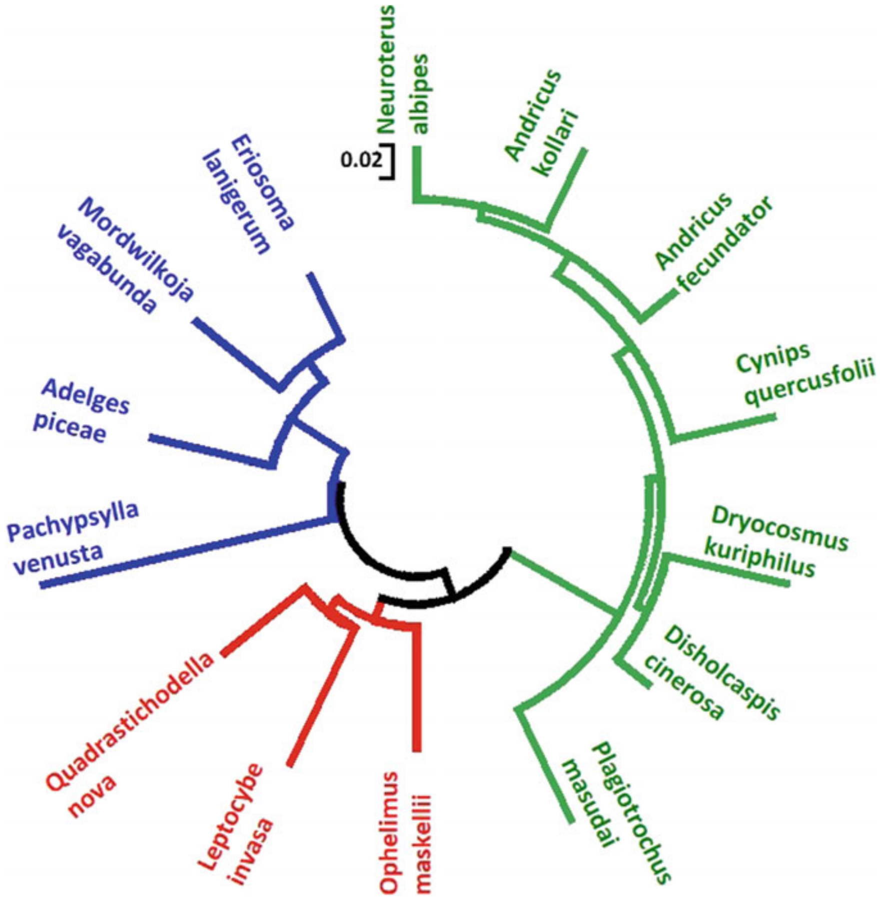

Fig. 14.1 A circular neighbour joining tree showing the relatedness of gall forming insects in forests. Cytochrome b sequences available for gall-forming insects associated with forest trees were downloaded from GenBank and used to generate the tree. Colours correspond to the insect family, namely Adelgidae, Aphididae and Psyllidae (*blue*); Cynipidae (*green*); and Eulophidae (*red*)

hosts (Ronquist et al. 2015). Kinsey (1920) hypothesized that gall formers initially utilized herbs as their hosts and inhabited the plant tissue rather than induced galls. These galls subsequently evolved and increased in complexity with for example multi-chambered galls, considered structurally simple, evolving into single chambered galls, considered structurally complex (Ronquist et al. 2015). This increased complexity over evolutionary time has also been observed in aphids, thrips and sawflies (Fukatsu et al. 1994; Nyman et al. 1998; Morris et al. 1999). Other authors such as Malyshev (1968) have argued that early cynipids were associated with oaks and first formed galls on buds or seeds. However, Roskam (1992) suggested that recent radiation events in the Oligocene led to the radiation of the cynipids from the family of flowering plants, the Asteraceae.

The three main advantages of development within galls are the availability of nutrition, a constant microclimate, and protection against parasitoids and herbivores due to physical and/or chemical features of the gall (Stone and Schönrogge 2003; Ronquist et al. 2015). It is generally accepted that the evolution of gall formers has largely been driven by selection pressure from natural enemies (Stone and Cook 1998) and to a lesser extent mistakes during oviposition/host selection by female gall formers (Price 2005). High mortality levels of gall formers, caused by parasitoids, has been suggested to drive the evolution of various morphological gall characteristics, such as gall size, thickness of gall exterior and spiny surfaces, in an attempt to decrease mortality levels (Inbar et al. 2004; Hardy and Cook 2010). This top-down force could be one of numerous factors driving variation in gall formation (Nosil and Crespi 2006). Parasitoids may parasitize gall formers on a preferred plant host, leading to the use of a new plant host by the gall former, in an attempt to evade mortality thereby resulting in variation in gall formation (Rott and Godfray 2000; Singer and Stireman 2005). Studies have shown that most often there is a correlation between gall morphology and relatedness of the gall former, however there are a few exceptions (Inbar et al. 2004).

Phylogenetic analyses suggest that most of the diversity making up the gall forming species, within for example the Cecidomyiidae and Cynipoidea, is due to a radiation event (the rapid splitting of a lineage into two distinct lineages, due to certain conditions which result in a new feature, permitting the lineage to access a new niche), rather than the independent acquisition of the gall forming trait (Ronquist and Liljeblad 2001). This conclusion is based on the occurrence of many gall forming species in only a few insect families, rather than gall forming species distributed amongst many insect families (Cook and Gullan 2004; Vardal 2004). Some groups of gall formers, such as the Cynipdae contain many species whereas others such as the Aphididae contain far less, possibly indicating that a large degree of speciation occurred within the Cynipidae at a rapid rate (Price 2005). Consequently, such groups are difficult to separate at a taxonomic level, as morphological characteristics are not distinctive enough to separate specimens into different genera.

Diversification of gall forming insects has been thought to be influenced and driven by individual phenotypic traits (e.g. reproductive rate, dispersal ability, body size, longevity, ecological constraint, sexual selection), species-specific traits (e.g. population size, abundance, geographic range), and availability of sufficient suitable hosts (Hardy and Cook 2010). The most likely factor contributing to speciation within gall-formers is the acquisition of a new host or plant organ (Medonça 2001). Due to the specificity of the relationship between the gall former to its host plant, the shift of a gall former to a new host is very rarely observed and rarely successful (Csóka et al. 2017). For this reason, no gall former has been recorded as utilising a wide range of host plants (Ronquist et al. 2015; Csóka et al. 2017).

Interestingly, within the Hymenoptera, the family Eulophidae contains species with diverse biologies, ranging from predominantly parasitoids to gall formers and seed feeders (Gauthier et al. 2000). The Eulophidae represents the largest group of parasitoids within the Chalcidoidea and contains over 4000 described species, including many that have been successfully used for biological control (Noyes 1998; Gauthier et al. 2000). The origin of parasitism is thought to have arisen from the group ancestral to the Orussoidea and Apocrita (Whitfield 1998). Early parasitoids evolved from hymenopterans feeding on both wood-boring larvae and to a lesser extent on fungi.

14.4 Gall Formers of Forest Trees

Gall forming insects are present on all continents except Antarctica and infest many forest tree species including both hardwood and softwood species. In some cases these infestations are not considered to significantly affect the health of the trees, whereas in other cases these insects are reported as serious pests. The majority have been reported from the northern hemisphere, but it is unclear whether this is a true reflection of higher diversity or if it is due to differences in reporting and research on these insects between the two hemispheres. We provide a summary of gall forming insects known to infest forest trees in Table 14.2, focusing on those that are considered as pests and/or which have been well studied.

Although gall forming insects that infest forest tree species are present in a number of insect orders and families, most of these insects are from the Adelgidae (Hemiptera), the Cecidomyiidae (Diptera), and the Cynipidae and Eulophidae (Hymenoptera) (Table 14.2). The Cecidomyiidae gall formers are associated with a range of host trees and gall types, including artichoke-shaped galls of some of the *Dasineura* species, spindle shaped galls at the base of pine needles, and galls which at maturity resemble a small flower on the branches. Nearly all of the adelgid gall formers belong to the genus *Adelges*. Several of these species have been shown to be holocyclic, where the primary host is always *Picea* and the secondary host is *Abies*, *Larix*, *Pseudostuga*, *Tsuga* or *Pinus*. These insects cause damage at the non-galling (asexual) stage, whereas the galling stage is not considered problematic. The galls resemble small pineapples.

Most of the Cynipidae are gall formers on oak species and associated with visually striking galls, sometimes with the appearance of apples. The oak gall wasps are also known to have complex communities of parasitoids and inquilines. An important cynipid that is not associated with oaks is the chestnut gall wasp, *Dryocosmus*

Table 14.2 Gall-forming insects of forest trees. This list is based on an extensive search of the available literature. It is not exhaustive, but provides an indication of the diversity of these insects. For 'Known Distribution', I = introduced range and N = native range (not known for all cases)

Species	Known distribution	Host	Gall type	References
Coleoptera: Cerambycidae				
Podapion gallicola (Pine gall weevil)	North America	*Pinus*	Spindle shaped stem galls	Drooz (1985), and Rose and Lindquist (1999)
Saperda inornata (Poplar gall saperda)	North America	*Populus* spp.	Globose galls on twigs and stems	Browne (1968), and Ciesla (2011)
Saperda concolor	North America	*Populus* spp.	Globose stem galls	
Saperda pupulnea (Small poplar borer)	Europe (N); China (N); North America (I); Canada (I)	*Populus* spp. especially on *P. nigra* & *P. tremula* in Turkey & *Salix* spp. (willows)	Globose stem galls	Ciesla (2011)
Diptera: Agromyzidae				
Hexomyza (=Melanagromyza) schineri (Poplar twig gall fly)	Northern Hemisphere	*Populus* spp. and *Salix* spp.	Spherical galls on new shoots which continue to grow as the tree grows	Browne (1968), and Ciesla (2011)
Diptera: Cecidomyiidae				
Contarinia pseudotsugae (Douglas-fir needle midge)	North America (I); Europe (I)	*Pseudotsuga menziesii* (Douglas-fir)	Yellowish galls on the needles	Bulaon (2005)
Dasineura gleditchiae (Honey locust gall midge)	North America (I); Europe (I)	*Gleditsia triacanthos* (Honey locust)	Pod-like galls on Individual leaflets: each gall contains 1–5 larvae	Molnár et al. (2009), and Csóka et al. (2017)
Dasineura kellneri	Central Europe	*Larix decidua*	Artichoke shaped galls on stems and flowering buds	Isaev et al. (1988), and Ciesla (2011)

(continued)

Table 14.2 (continued)

Species	Known distribution	Host	Gall type	References
Dasineura nipponica	Japan	*Larix kaempferi*	Artichoke shaped galls on stems and flowering buds	Isaev et al. (1988), and Ciesla (2011)
Dasineura rozhkovi	Europe; Asia	*Larix czekanowski, L. gmelinii & L sibirica*	Artichoke shaped galls on stems and flowering buds	Isaev et al. (1988), and Ciesla (2011)
Dasineura strobilas	Australia	*Leptospermum laevigatum* (Coastal tea tree) (Myrtaceae)	Artichoke shaped galls on stems and flowering buds	Isaev et al. (1988), and Ciesla (2011)
Dasineura verae	Europe; Asia	*L. gmelinii & L sibirica*	Artichoke shaped galls on stems and flowering buds	Isaev et al. (1988), and Ciesla (2011)
Obolodiplosis robiniae	Europe; South Korea; Japan; Russia	*Robinia pseudoacacia* (North American Black Locust)	Downward-folded swellings	Molnár et al. (2009), and Csóka et al. (2017)
Oligotrophus apicis	Central America	*Juniperus* spp.	Blue/green apical conical galls resembling a small flower which turns red/brown as it matures on branches	Ciesla (2011)
Oligotrophus betheli (Juniper tip midge)	North America (N); British Columbia (I); Canada (I)	*Juniperus* spp. *J. occidentalis*, *J. osteosperma*, *J. scopulorum* & *J. virginiana*	Blue/green apical conical galls resembling a small flower which turns red/brown as it matures on branches	Ciesla (2011)
Oligotrophus gemmarum	Europe	*Juniperus* spp.	Blue/green apical conical galls resembling a small flower which turns red/brown as it matures on branches	Ciesla (2011)

(continued)

Table 14.2 (continued)

Species	Known distribution	Host	Gall type	References
Oligotrophus juniperinus	Europe	*Juniperus* spp.	Blue/green apical conical galls resembling a small flower which turns red/brown as it matures on branches	Ciesla (2011)
Oligotrophus nezu	Japan	*Juniperus* spp.	Blue/green apical conical galls resembling a small flower which turns red/brown as it matures on branches	Ciesla (2011)
Oligotrophus panteli	Europe	*Juniperus* spp.	Blue/green apical conical galls resembling a small flower which turns red/brown as it matures on branches	Ciesla (2011)
Paradiplosis tumiflex (Balsam gall midge)	Canada (I); North America (N)	*Abie balsamea* (Balsam fir) and *Abies fraseri* (Fraser fir)	Oval galls on the needles	Drooz (1985), and Ciesla (2011)
Taxodiomyia cupressiananassa (Cypress twig gall midge)	North America; Central America	*Taxodium distichum* (Bald cypress)	Oval galls on terminal portion of branchlets which resemble pineapples at maturity; pink in colour which changes to green/white	Chen and Applybyby (1984), and Ciesla (2011)
Thecodiplosis jaonensis (Pine needle gall midge)	Japan (N); South Korea (I); North Korea (I)	*Pinus densiflora* & *P. thunbergii*	Spindle shaped galls on the base of needles	Ciesla (2011)

(continued)

Table 14.2 (continued)

Species	Known distribution	Host	Gall type	References
Pinyonia edulicola (Pinon spindle gall midge)	North America	*Pinus edulis* (Pinon pine)	Spindle shaped galls base of current years needles	Ciesla (2011)
Rhabdophaga rosaria	Europe	*Salix* spp. *Salix alba*	Pine cone shaped gall	Kollár (2007), and Ciesla (2011)
Rhabdophaga strobiloides (Willow pine cone gall)	North America (N); South America (I); Central America (I)	*Salix* spp.	Pine cone shaped bud gall (25 mm)	Kollár (2007), and Ciesla (2011)
Hemiptera: Adelgidae				
Adelges abietis (Eastern spruce gall adelgid)	Europe (N); North America (I)	*Picea* spp.	Spherical to small pineapple/conelike galls (10–18 mm long) on the base of new twigs, size and shape varies depending on hosts	Carter (1971), and Ciesla (2011)
Adelges cooleyi (Cooley spruce gall adelgid)	North America (N); Europe (I)	*Picea* spp. *Picea sitchensis* (Sitka spruce)(primary host where galls induced); *Pseudotsuga* species (*Pseudotsuga menziesii* - Douglas fir)	Small light green to dark purple pineapple shaped galls on shoots and needles	Havill and Foottit (2007), and Csóka et al. (2017)
Adelges glandulae	China	*Picea* (primary host) & *Abies* (secondary host)	Leaf cone-like gall without associated needles	Zhang et al. (1980), and Havill and Foottit (2007)
Adelges isedakii	Japan	*Picea* (primary host) & *Larix* (secondary host)	Cone-like gall	Havill and Foottit (2007), and Ciesla (2011)

(continued)

Table 14.2 (continued)

Species	Known distribution	Host	Gall type	References
Adelges japonicus	Japan	*Picea* (primary host) & Abies (secondary host)	Cone-like gall	Ciesla (2011)
Adelges knucheli	South Asia	*Picea* (primary host) & *Larix kaempferi* (secondary host)	Cone-like gall	Ciesla (2011)
Adelges lapponicus	Europe	*Picea* (primary host) & *Larix decidua* (secondary host)	Cone-like gall	Ciesla (2011)
Adelges lariciatus	Eastern North America (N); Canada (I)	*Picea* (primary host)	Buds and cones	Ciesla (2011)
Adelges laricis	Europe	*Picea* (primary host) & *Larix laricina & L. lyallii* (secondary host)	Small pineapple shaped galls of shoots and needles	Carter (1971)
Adelges merkeri	Asia Minor (N); Europe (I)	*Albies* (secondary host)	Cone-like gall	Havill and Foottit (2007), and Csóka et al. (2017)
Adelges nebrodensis	Europe	*Picea* (primary host) & Abies (secondary host)	Cone-like gall	Ciesla (2011)
Adelges nordmanniana	North America (N); Europe (I); Australia (I); New Zealand (I)	*Picea* spp. (primary) & *Abies nordmanniana* (secondary host)	Cone like galls	Ciesla (2011), and Csóka et al. (2017)
Adelges normannianae	North America (N); Europe (I)	*Picea orientalis* (primary host); *Albies* (secondary host)	Cone-like galls of shoots and needles on primary host; curling and thickening of needles (similar to bottlebrush) on secondary host	Carter (1971)

(continued)

Table 14.2 (continued)

Species	Known distribution	Host	Gall type	References
Adelges pectinata	Europe, China and Japan	*Picea* (primary host) & Abies (secondary host)		Ciesla (2011)
Adelges piceae (Balsam woolly adelgid)	Central Europe (I); North America (I)	*Abies* (true firs): *A. balsamea* and *A.fraseri* (Balsam and Fraser)	Swellings and thickening of shoots and needles	Carter (1971), and Ciesla (2011)
Adelges prelli	North America (N); Europe (I)	*Picea* spp. (primary) & *Pinus* (secondary host)	Cone-like gall	Ciesla (2011), and Csóka et al. (2017)
Adelges tardoides	Europe	*Picea* (primary host) & *Larix* (secondary host)	Cone-like gall	Ciesla (2011)
Adelges torii	Japan	*Picea* (primary host) & *Larix* (secondary host)	Cone-like gall	Ciesla (2011)
Adelges tsugae (Hemlock woolly adelgid)	Asia and western North America (N); eastern North America (I)	*Picea* (Primary host in native range); *Tsuga (secondary host)*	Small pineapple shaped galls of shoots and needles	Ciesla (2011)
Adelges viridis	Europe	*Picea* (primary host) & *Larix decidua* (secondary host)	Cone-like gall	Ciesla (2011)
Pineus pinifoliae (Pine leaf adelgid/chermes)	North America (N)	*Picea* spp.	Loose, terminal and leafy cone-shaped galls on young shoots	Drooz (1985)
Hemiptera: Aphididae				
Eriosoma lanigerum (Woolly apple aphid)	North America (N); South Africa (I); Australia (I)	*Malus pulima* (Apple) & *Pyrus* (pear)	Root and swollen and twisted twig galls	Nicholas et al. (2005)

(continued)

Table 14.2 (continued)

Species	Known distribution	Host	Gall type	References
Mordvilkoja vagabunda (Poplar vagabond aphid)	North America (N); Canada (I); Turkey (I)	*Populus* (primary host); *Lythrum* spp. (Loosestrife) (alternative host)	Large and convoluted green or brown galls (5–7 cm) on the tips of shoots	Ciesla (2011)
Pachypsylla celtidisgemma (Budgall psyllid)	North America	*Celtis occidentalis* (Hackberry)	Small round bud galls	Riley (1885)
Pachypsylla venusta (Petiolegall psyllid)	North America	*Celtis occidentalis* (Hackberry)	Woody subspherical petiole galls	Johnson and Lyon (1988)
Pachypsylla celtidisvesicula (Hackberry blister gall maker)	North America	*Celtis occidentalis* (Hackberry)	Blister-like galls (3–4 mm diameter and slightly raised) on the leaf surface	Johnson and Lyon (1988)
Pachypsylla celtidismamma (Hackberry nipple gall maker)	North America	*Celtis* sp. (Hackberry) especially *Celtis occidentalis*	Small round yellow to yellow-green galls (4 mm diameter and 6 mm high)	Drooz (1985), and Ciesla (2011)
Pemphigus populivenae (Sugarbeet root aphid)	Europe; North America	*Celtis laevigata* (Sugarbeets)	Elongated root galls	Foottit et al. (2010)
Hemiptera: Homotomidae				
Phytolyma fusca	Tropical Africa	*Milicia* sp. especially *M. excelsia*	Leaf galls are globular in shape; galls on the stems and shoots are oblong in shape	Wagner et al. (2008), and Ciesla (2011)
Phytolyma lata (Iroko gall fly)	Tropical Africa	*Milicia* sp. especially *M. regia*	Shoot, bud and leaf galls	Hollis (1973), and Cobbinah (1986)
Phytolyma tuberculate	Tropical Africa	*Milicia* sp. especially *M. excelsia*		Hollis (1973)
Hymenoptera: Cynipidae				
Amphibolips californicus	North America	*Quercus alba* (White oak)	Apple galls	

(continued)

Table 14.2 (continued)

Species	Known distribution	Host	Gall type	References
Amphibolips confluenta (Oak apple gall wasp)	Australia (N); North America (I)	*Quercus* spp. (Oaks) *Q. coccinea*, *Q. rubra* & *Q. velutina*	Large green apple galls which are quite robust; become brown as they mature	Drooz (1985)
Andricus quercuscalifornicus (=*californicus*) (California gall wasp)	North America	*Quercus garryana*	Apple gall (asexual)	Drooz (1985)
Andricus corruptrix	South Eastern Europe (N); Britain & British Isles (I)	*Quercus robur, Quercus cerris* & *Quercus petraea*	Single cone-shaped gall with a darkened point (sexual); irregular shaped, smooth gall with 3–5 lobed tip (asexual)	Schönrogge et al. (1996, 2012)
Andricus lucidus	South Eastern Europe (N); Britain & British Isles (I)	Sexual: *Quercus cerris. Asexual:* Q.robur & Q. petreae	Groups of bright yellow-green apple galls	Schönrogge et al. (2012)
Andricus grossulariae	South Eastern Europe (N); Britain & British Isles (I)	Sexual: *Quercus cerris. Asexual:* Q.robur & Q. petreae	Unilocular deep purple rounded galls (usually clustered) on catkin (bisexual); green-purple galls which are spined (asexual)	Schönrogge et al. (1996, 2012)
Andricus kollari	South Eastern Europe (N); Britain & British Isles (I)	*Quercus robur, Quercus petraea* & *Quercus cerris*	1–8 thin pointed galls per bud and occasionally have tufts of hair on the upper part (bisexual); hard, round and smooth small red-brown globular bumps on the bud (marble gall) (asexual)	Schönrogge et al. (1996, 2012)

(continued)

Table 14.2 (continued)

Species	Known distribution	Host	Gall type	References
Andricus lignicola	South Eastern Europe (N); Britain & British Isles (I)	*Quercus robur, Quercus cerris* & *Quercus petraea*	1–8 golden/brown galls with plunt rounded tip on a bud (bisexual); leathery brown globular bud gall (asexual)	Schönrogge et al. (1996, 2012)
Andricus lucidus (Hedgehog gall)	South Eastern Europe (N); Britain & British Isles (I)	*Quercus robur, Quercus cerris* & *Quercus petraea*	Bright green galls aggregated together (bisexual); rounded gall covered in spines (hedgehog gall) (asexual)	Chinery (2011)
Andricus quercuscalicis (Knopper gall wasp)	South Eastern Europe (N); Britain & British Isles (I)	*Quercus robur* (English Oak) & *Quercus cerris* (Turkey Oak)	Slender pointed single galls on the male flowers of Turkey Oak (bisexual); irregular gall which appears around the acorns of English Oak (knopper gall) (asexual)	Schönrogge et al. (1996, 2012)
Aphelonyx cerricola	South Eastern Europe (N); Britain & British Isles (I)	*Quercus cerris*	Large irregularly shaped galls which appear green and velvety and become brown and woody; neighbouring galls often fuse together	Crawley (1997), and Schönrogge et al. (2012)
Biorhiza pallida	Europe	*Quercus* spp. (Oaks)	Spongy apple bud gall (bisexual); spherical root galls (asexual)	Drooz (1985)
Callirhytis tumifica	North America (N); Europe (I)	*Quercus rubra* (planted in other countries as plantation trees), *Q. palustris, Q. coccinea, Q. schumardi,* etc. (North American red oaks)	Acorn (asexual); leaves (bisexual)	Csóka et al. (2017)

(continued)

Table 14.2 (continued)

Species	Known distribution	Host	Gall type	References
Callirhytis cornigera (Horned oak wasp)	Canada; North America	*Quercus palustris* (Pin Oak)	Golf ball sized woody stem galls with horn-like protrusions (asexual) and small blister-like leaf galls (bisexual)	Felt (1917)
Callirhytis quercusclaviger	Canada; North America	*Quercus laurifolia* (Laurel Oak)	Woody stemmed potato galls bearing spines (Spine bearing Potato Gall)	Felt (1917)
Callirhytis quercuspomiformis (=pomiformis) (live oak apple gall wasp)	Great Britain; North America	*Quercus agrifolia* (California live oak)	Large apple type galls with a gnarled surface (asexual); leaf galls (bisexual)	
Cycloneuroterus hisashii	Japan	*Quercus (Cyclobalanopsis) glauca*	Globular bud gall	Ide et al. (2012)
Cycloneuroterus arakashiphagus	Japan	*Quercus (Cyclobalanopsis) sessilifolia; Quercus (Cyclobalanopsis) glauca*	Clustered pale green/yellowish brown oval bud gall (asexual); leaf galls (sexual)	Ide et al. (2012)
Cycloneuroterus akagashiphilus	Japan	*Quercus (Cyclobalanopsis) acuta*	Oval gall on margin/apex of young leaves	Ide et al. (2012)
Cycloneuroterus fortuitusus	Japan; Taiwan	*Quercus (Cyclobalanopsis) sessilifolia; Quercus (Cyclobalanopsis) glauca*	Oval galls at the base of young shoots and buds	Ide et al. (2012)
Cycloneuroterus wangi	South eastern China; Japan	*Quercus (Cyclobalanopsis) sessilifolia*	Bud galls	Mendel et al. (2004)
Cynips longiventris	Europe; Asia	*Quercus* spp.		

(continued)

Table 14.2 (continued)

Species	Known distribution	Host	Gall type	References
Cynips divisa	Europe; Asia	*Quercus* spp.	Thin walled round pall yellow galls which have red-brown markings (asexual); bright yellow–brown smooth gall (red-wart gall) (bisexual)	Browne (1968)
Cynips insana		*Quercus infectoria*		Fagan (1918), and Felt (1940)
Cynips quercusfolii (oak bud wasp)	Asia	*Quercus* spp. most commonly found on *Q. petraea* and *Q. robur*	Small, ovoid galls which begin as a deep red/purple colour and turn black as the gall matures (violet-egg gall) (bisexual); spherical yellow/green–brown hard and brittle leaf galls (asexual)	Ciesla (2011)
Disholcaspis cinerosa	North America	*Quercus fusiforme* & *Q. virginiana*	Sexual generation: inconspicuous galls on the bud; Asexual generation: large ranging from 3 to 25 mm on the stem	Ciesla (2011)
Disholcaspis quercusmamma (rough oak bullet gall wasp)	Central America	*Quercus bicolor* (Swamp white oak) & *Q. macrocarpa* (Burr Oak)	Round woody galls with a point at the apex these galls change to red/brown colour as maturation occurs; galls remain on the branch for several years after the insect has left	Ciesla (2011)

(continued)

Table 14.2 (continued)

Species	Known distribution	Host	Gall type	References
Dryocosmus kuriphilus (Chestnut gall wasp)	China (N); Japan (I); North America (I); Europe (I)	*Castanea*spp. China: *C. mollissim.* Korea & Japan: *C. crenata* & *C. crenata* x *C. mollissim.* USA: *C. mollissima.* Italy: *C. denata* (native to Italy)	Rose-coloured bud gall	Moriya et al. (1989a), and Csóka et al. (2017)
Neuroterus saliens	Britain & British Isles	*Sexual: Quercus cerris. Asexual: Q.robur & Q. petreae*	Uniocular green–brown pimple-like leaf galls (asexual); red multi-ocular acorn galls with disc-like eruptions (bisexual)	Schönrogge et al. (2012), and Csóka et al. (2017)
Neuroterus saltatorius (Jumping oak gall wasp)	North America	White Oaks: *Quercus lobata* (Valley oak), *Quercus douglasii* (blue oak), *Quercus garryana* (Oregon or Garry oak), Quercus dumosa (California scrub oak), *Quercus arizonica* (Arizona white oak), *Quercus virginiana* (Live oak)	Sexual: non-detachable cluster galls, galls are originally green and turn brown as they mature; asexual: small mustard coloured sub-spherical galls, single chamber and detachable from leaf	Csóka et al. (2017)
Plagiotrochus coriaceus/Andricus pseudococcus	Britain & British Isles	*Quercus ilex*	Uniocular oval leaf gall	Schönrogge et al. (2012)
Plagiotrochus quercuscalis	Britain & British Isles	*Quercus ilex*	Bud gall	Hancey and Hancey (2004), and Schönrogge et al. (2012)

(continued)

Table 14.2 (continued)

Species	Known distribution	Host	Gall type	References
Plagiotrochus amenti	southwest Europe (N) and northwest Africa (N); Europe (I); North America (I); South America (I)	*Quercus suber* (Cork oak)	Sexual generation: catkins & shoots. Asexual generation: underneath the bark of 2–3 year old twigs	Csóka et al. (2017)
Plagiotrochus australis	United Kingdom	*Quercus ilex*	Sexual generation: galls in the leafblade. Asexual: galls beneath the bark of twigs	Schönrogge et al. (2012)
Plagiotrochus masudai	Taiwan	*Quercus glauca*	Bud galls	
Trichoteras vaccinifoliae	North America	*Quercus chrysolepis* (canyon live oak)	Oak apple gall (30 mm) with small red dots	
Hymenoptera: Eulophidae				
Epichrysocharis burwelli	Asia; North America; South America	*Eucalyptus*	Numerous blister galls on the leaves	Schauff and Garrison (2000)
Leptocybe invasa (Blue gum chalcid) - Haplogroup 1/Lineage A	Australia (N); Mediterranean (I); south eastern Europe (I); Asia (I); southern Asia (I); South America(I)	*Eucalyptus*	Rounded pink - red protrusions on the midrib of leaf, petiole, stem, and young shoots	Csóka et al. (2017), Nugnes et al. 2015, and Dittrich-Schröder et al. 2018, 2020)
Leptocybe invasa (Blue gum chalcid) - Haplogroup 2/Lineage B	Australia (N); Asia(I); Africa (I); South East Asia (I)	*Eucalyptus*	Rounded pink - red protrusions on the midrib of leaf, petiole, stem, and young shoots	Nugnes et al. (2015), and Dittrich-Schröder et al. (2018, 2020)
Moona spermophaga	Australia (N); Africa(I); South America(I)	*Corymbia maculata* (spotted gum)	Seed galls	Kim et al. (2005)

(continued)

Table 14.2 (continued)

Species	Known distribution	Host	Gall type	References
Ophelimus maskelli	Australia (N); Africa (I), Asia (I), Europe (I), North America (I)	*Eucalyptus*	Blister-type galls on the leaf midrib and young shoots	Csóka et al. (2017)
Ophelimus eucalyptii (Eucalyptus gall wasp)	Australia (N); New Zealand (I); Mediterranean (I): Europe (I); Middle East (I) and Africa (I)	*Eucalyptus* spp. In New Zealand: *E. botryoides*, *E. deanei*, *E. grandis, E. saligna, E. camuldulensis* and *E. globulus*	Female larvae produce a circular protruding galls on the leaves; male larvae produce a pit gall	Withers et al. (2000), and Raman and Withers (2003)
Ophelimus migdanorum	China; South America (I)	*Eucalyptus*	Blister-type galls on the leaf surface and stems	Molina-Mercader et al. (2019)
Ophelimus mediterraneus	Australia (N); Europe (I); Mediterranean (I)	*Eucalyptus*	Brown coloured ellipsoid shaped galls on the upper leaf surface	Borowlec et al. (2018)
Quadrastichus erythrinae (Erythrina gall wasp)	Africa (N: some uncertainty); China (I); North America (I); South Asia (I); South East Asia (I); Taiwan (I)	*Erythrina* (tiger's claw & Indian coral)	Tiny green globular galls in large numbers on the leaflets and petioles	Csóka et al. (2017)
Quadrastichodella nova	Africa; Europe; South America;North America	*Eucalyptus*	Fully developed flowers and flower buds	Klein et al. (2015)
Selitrichodes globulus (Bluegum gall wasp)	Australia (N); North America (I)	*Eucalyptus globulus* (Blue gum)	Multiple small brown galls on the branches and sometimes the leaves	La Salle et al. (2009)
Hymenoptera: Eurytomidae				
Eurytoma tumoris	North America	Scot's pine Christmas tree	Terminal and lateral branches	Smith (1968), and Ciesla (2011)

(continued)

Table 14.2 (continued)

Species	Known distribution	Host	Gall type	References
Hymenoptera: Pteromalidae				
Nambouria xanthops	New Zealand	*Eucalyptus*	Irregular shaped gall resembles a comb on the leaves	Berry and Withers (2002)
Hymenoptera: Tenthredinidae				
Euura shibayanagii	Japan	*Salix japonica* (exclusively on this species)	Bud galls have a swollen appearance; stem galls tend to be narrow and bulbous; colouration varies from white, dark green, red or red-brown	Ciesla (2011)
Euura mucronata	North Africa; North America; Southeast Asia	*Salix* spp. (at least 30 species)	Bud galls have a swollen appearance; stem galls tend to be narrow and bulbous; colouration varies from white, dark green, red or red-brown	Nyman (2002)
Euura exigue	North America	*Salix* spp. (Willows)	Elongated stem galls	Bugbee (1970)
Pontania proxima (Willow red gall sawfly)	Australia; Europe; India and North America	*Salix* spp. (willows)	Conspicuous, red, round and often occur in clusters on the leaves	Smith (1968), and Ciesla (2011)
Lepidoptera: Olethreutidae				
Proteotera willingana (Boxelder twig borer)	North America	Maple	Spindle-shaped galls on dormant leaf buds	Kearfott (1904)

kuriphilus. This insect is native to China, but has been introduced into other parts of Asia, North America and Europe where it infests chestnut trees and can cause substantial damage. Of the Eulophidae, the best-known species are *Leptocybe invasa*, *Ophelimus maskeli* and *O. eucalypti*, all of which are invasive pests of *Eucalyptus* (Dittrich-Schröder et al. 2020).

Gall forming insects of forest tree species are less common in the orders Coleoptera and Lepidoptera. Examples include the poplar gall *Saperda inornata* (Coleoptera: Ceramycidae) and the boxelder twig borer, *Proteotera willingana* (Lepidoptera: Olethreutidae), which infest poplar and maple in North America, respectively (Table 14.2). Other families which include gall forming insects on forest trees include Agromyzidae in the Diptera; Aphidae and Homotomidae in the Hemiptera; Eurytomidae, Pteromalidae and Tenthredinidae in the Hymenoptera.

14.5 Management

In cases where gall insects become serious pests on forest trees, a number of management options exist. Chemical control is of limited use as the majority of the insect's life cycle is protected within the gall. Systemic insecticides may be effective in a small number of cases. For example, stem injections of individual trees are used to control the hemlock woolly adelgid, *Adelges tsugae* (Csóka et al. 2017). However, the use of systemic insecticides is generally not a financially feasible option for large areas of forest (i.e. in natural or plantation forests).

Natural enemies of gall forming insects can assist to maintain populations at low levels. Although the natural enemies of many of the gall forming insects are not known, where they have been studied, gall formers have often been found to have a number of parasitoids (Table 14.1). For invasive gall insects a classical biological control (CBC) approach has often been used, as is the case with the eucalypt-infesting gall wasps, *L. invasa* and *O. maskelli* (Protasov et al. 2007; Kim et al. 2008; Dittrich-Schröder et al. 2014). There are no known parasitoids of adelgid gall formers, and thus biological control programmes for these gall formers have focused on pathogens and predators.

Host genetic selection is a management approach that is often used in plantation forests. Here, more resistant species or genotypes are planted, replacing those that are more susceptible. This approach can include in field or nursery screening trials (Dittrich-Schröder et al. 2012) in addition to research elucidating the mechanisms behind host resistance (Oates et al. 2015, 2016). This approach can be very successful to control gall insects due to their high host specificity.

It is important to note that most gall forming insects that infest forest trees are not considered pests, and of those that are considered pests, many are not of economic concern and thus do not require management. This is partly because most gall forming insects have not established outside their native range, and within their native range their impact is limited by bottom-up (e.g. host resistance) and top-down (e.g. natural enemies) factors. For example, although there has been much study on the parasitoid community of the oak gall wasps, *Andricus* spp. (Stone and Sunnucks 1993; Stone et al. 1995) (see Case Study 14.6.2), biological control programmes for these wasps has not been necessary. Native gall forming insects can still become serious pests, but it is often the non-native introduced species that require management intervention. This has been the case with the gall wasps of *Eucalyptus*, such as *Leptocybe invasa* (see Case Study 14.6.3).

14.6 Case Studies

14.6.1 Adelges cooleyi *(Gillette 1907), Cooley Spruce Gall Adelgid (Adelgidae, Hemiptera)*

The Cooley Spruce Gall Adelgid (Fig. 14.2) is native to Western North America and reproduces by cyclical parthenogenesis (Havill and Foottit 2007). Cyclical parthenogenesis may be defined as "several rounds of clonal reproduction followed by a sexual event" (Rouger et al. 2016). The duration of the entire life cycle is two years. This species is holocyclic, which refers to the occurrence of sexual reproduction in at least one of the generations, whereas reproduction during the other generations is parthenogenic. A characteristic of holocyclic species is the use of alternate hosts to complete their life cycle. *Adelges cooleyi* has five distinct generations of which three occur on its primary host, spruce (*Picea sitchensis, Picea pungens* and *Picea engelmanii*), and two occur on its secondary hosts Douglas fir and the bigcone Douglas fir (*Pseudotsuga menziesii* and *Pseudotsuga macrocarpa*). Holocyclic species form galls on their primary host and utilise their secondary host to support the parthenogenetic generations (Havill and Foottit 2007).

Winged adelgids, also known as sexupare, move from their secondary host to their primary host where they lay a single clutch of eggs. Thereafter, the sexupare die and the eggs are sheltered by their wings until they hatch. Male and female offspring are wingless and feed at the emergence site until the end of the fourth instar (Havill and Foottit 2007). Moulting occurs and the adult generation move towards the centre of the tree where they mate (Havill and Foottit 2007). Thereafter a large single egg is laid which gives rise to a wingless form, known as a fundatrix. The fundatrix selects a bud where she will overwinter until spring. At the onset of spring she feeds on the sap of the bud thereby initiating gall formation. Once the fundatrix is mature she produces a cluster of eggs that hatch into brown nymphs. These nymphs or gallicolae crawl into and feed inside the gall. The size of the gall is an indication of the number of nymphs present, with large galls containing more nymphs than smaller galls (Sopow and Quiring 2001). At the onset of summer the gall opens, allowing the gallicolae to emerge and moult into adults (Havill and Foottit 2007). This generation is winged allowing the gallicolae to disperse to their secondary host to lay eggs. The offspring emerging from these eggs are referred to as exules and are parthenogenic females. A portion of these exules, the progredientes, reproduce by

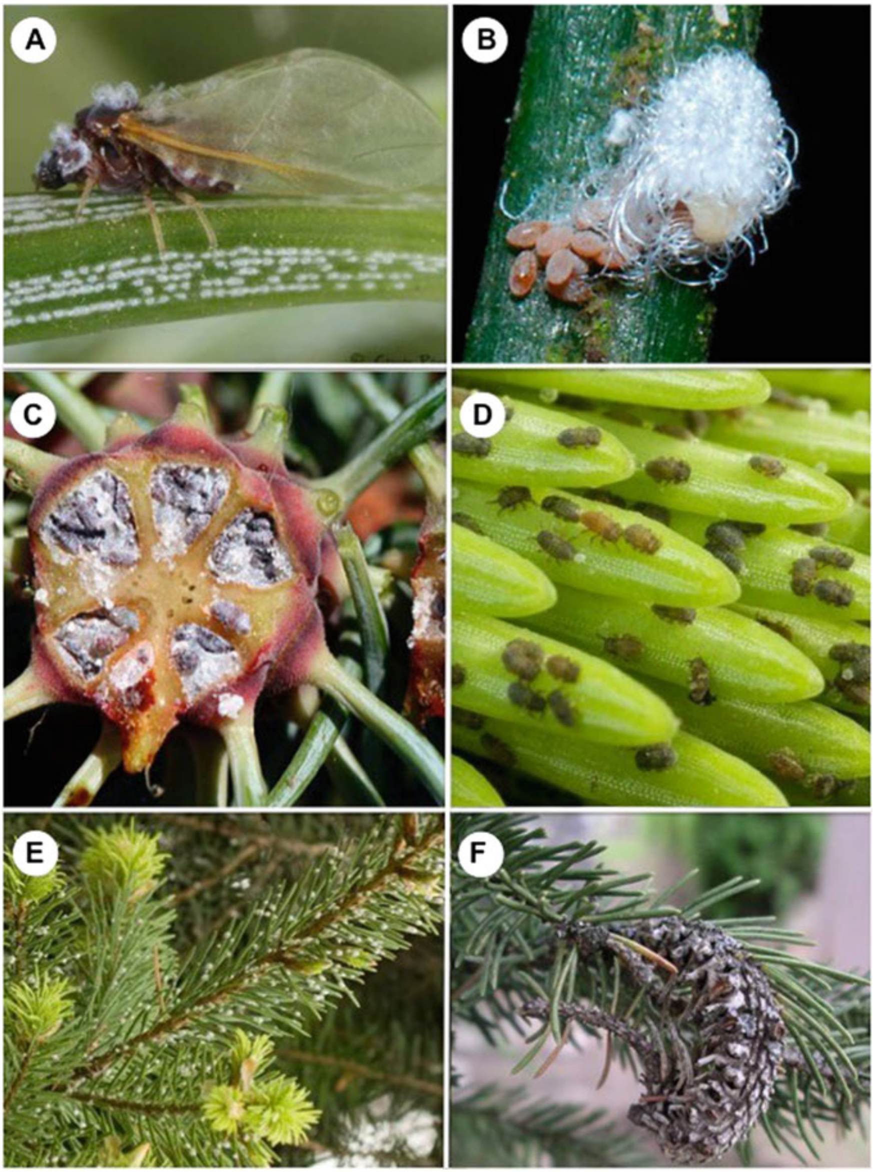

Fig. 14.2 The Cooley Spruce Adelgid, *Adelges cooleyi*: **A** winged female; **B** adult sistens with egg mass; **C** gallicolae feeding inside gall chambers; **D** nymphs; **E** Douglas fir infested with *Adelges cooleyi*; **F** old hardened gall case. Photo credits: **A** © Image, copyright Claude Pilon/Les Hemipteres du Quebec – pucerons all rights reserved, **B** © http://influentialpoints.com/Gallery/Adelges_cooleyi_Douglas_fir_adelgid_Cooley_spruce_gall_adelgid.htm#identi, **C** © courtesy of Whitney Cranshaw, Colorado State University / copyright Bugwood.org, **D** and **E** © D. Manastyrski/Cone and Seed Insect Pest Leaflet No. 14, **F** © Courtesy Ies, licensed under the Creative Commons Attribution 3.0 United States license/https://creativecommons.org/licenses/by/3.0/us/legalcode

parthenogenesis whereas others, the sistentes, overwinter on their secondary host. After overwintering, sistentes start feeding in early spring and produce waxy hair-like protrusions. They lay eggs which give rise to both winged and wingless offspring. The wingless generation remains on the secondary host whereas the winged generation return to their primary host where they produce both male and female offspring.

Damage on the primary host, spruce, is mainly aesthetic however severe gall-formation on the branch tips may lead to mortality of the growing tips. The feeding activities of *A. cooleyi* nymphs on the secondary host, Douglas fir and big-cone Douglas fir, cause needle discolouration and may cause the dropping of needles. As a result of the honey dew excreted by the feeding nymphs, black sooty mould may develop. Large numbers of adelgids may lead to a reduction in seed production.

Natural predators, such as lacewings, assassin bugs and lady beetles, are an important component of adelgid control. The effectiveness of insecticidal control is limited due to the waxy hair-like covering protecting many life stages of the insect. Short periods in the life cycle of adelgids are suitable for use of insecticidal soap, such as the emergence of nymphs from the eggs. Management approaches include ensuring that both primary and secondary hosts are not planted in close proximity.

14.6.2 Andricus spp., Andricus Gall Wasps (Cynipidae, Hymenoptera)

The oak gall wasps belong to the tribe Cynipini (Cynipidae: Hymenoptera) and are characterized by their heterogonic (cyclically parthenogenic) life cycle. Each species produces an asexual and bisexual generation that have morphologically distinct galls associated with the plant family Fagaceae, specifically on *Quercus* (oaks) (Cook et al. 2002). There are approximately 1000 known species of oak gall wasps, of which the *Andricus* genus (Fig. 14.3) is one of the largest and most ecologically diverse (Cook et al. 2002). Species from this genus exhibit a lifecycle that involves two generations per year: sexual in spring and asexual (agamic) in autumn (Fig. 14.4). Each generation is specific with regards to the host species and the plant organ it attacks. Thus cynipids such as *Andricus*, which have a heterogonic life cycle, are restricted to the areas which contain both its hosts; this prerequisite is important in determining their patterns of global distribution (Stone et al. 2002).

There are four host-altering gall wasps from the genus *Andricus* (*Andricus corruptrix, A. kollari, A. lignicola* and *A. quercuscalicis*) that are native to south-eastern Europe but have become invasive in Britain since 1934. The sexual generation of these species occurs in spring on *Quercus cerris* (Turkey oak) and the asexual generation in autumn on *Q. robur* (English oak) and *Q. petreae* (sessile oak) (Schönrogge et al. 1998). *Quercus cerris* is a necessary secondary host for these gall wasps and their invasion was likely facilitated by its introduction into Britain (Schönrogge et al. 1998). *Quercus cerris* has been planted further north and west from its native range and this has created patches where it co-occurs with other *Quercus* species native

Fig. 14.3 The oak gall wasps, *Andricus* spp. **A** agamic gall induced by *A. quercuscalicis* (Knopper gall); **B** agamic gall induced by *A. kollari*; **C** agamic gall induced by *A. lignicola*; **D** agamic gall induced by *A. corruptrix*. Photo credits: **A**, **B** and **C** © David Fenwick/http://www.aphotofauna.com; **D** © Saxifraga – Frits Bink

to those areas (Stone et al. 2002). As a consequence of anthropogenic activity and the ability of *Q. cerris* to self-seed, it is likely that the area containing the necessary hosts to support the spread of *Andricus* wasps will increase (Stone and Sunnucks 1993; Walker et al. 2002).

As mentioned above, heterogonic life cycles are used by gall formers from many insect families. This mode of reproduction consists primarily of an annual agamic generation with a single sexual generation prompted by environmental cues (Stone et al. 2002). The heterogonic reproduction of the Cynipid wasps in general is unusual because of the strict alternation between sexual-agamic generations. As mentioned above, the gall which contains the sexual generation in oak gall wasps develops during the spring on *Quercus cerris*. After emergence from these galls, females mate and then oviposit on either *Q. robur* or *Q. petreae*. The resulting galls produce the asexual generation. In autumn, these females emerge and oviposit eggs on *Q. cerris,* which are dormant until spring the following year and the cycle begins again (Fig. 14.4). Deviations occur from this general pattern depending on the species and environmental conditions (Stone et al. 2002). The life-cycle of *A. kollari* alters depending on where it is geographically situated, in southern Europe it follows an annual life cycle, whereas in northern Scotland its development takes two years.

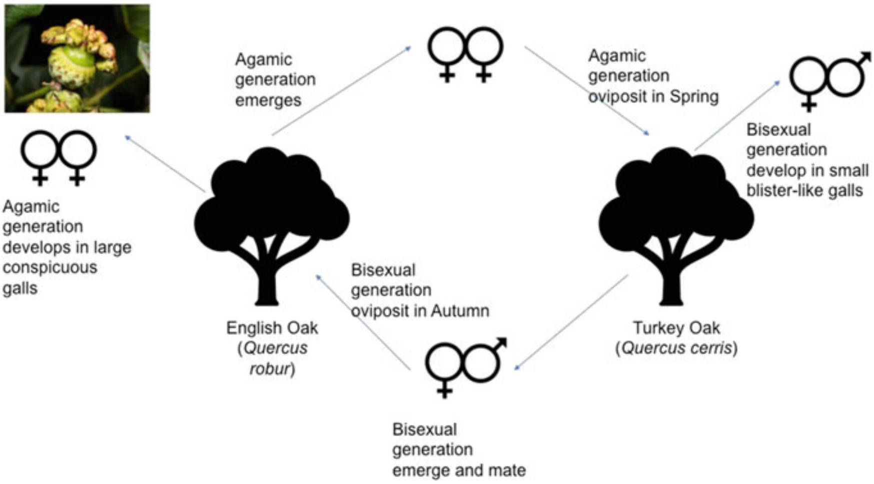

Fig. 14.4 An annotated diagram illustrating the heterogonic life cycle of the four invasive *Andricus* wasps (*Andricus corruptrix, A. kollari, A. lignicola* and *A. quercuscalicis)* described in this case study. This is a generalized depiction of the life-cycle, each species have slight deviations from the general rule, such as the organ choice. The agamic female wasp oviposition occurs in spring, the bisexual generation develops in the small blister-like galls. The bisexual generation mates and oviposits in Autumn, where the agamic females develop in large conspicuous galls. They alter between two hosts. Inset image of the *Andricus quercuscalicis* (Knopper) agamic gall. Photo credit: David Fenwick/http://www.aphotofauna.com). The Diagram was constructed by one of the authors, C. Gevers

Andricus corruptrix, *A. lignicola* and *A. kollari* induce galls on buds in both their sexual and agamic generations. In spring, the sexual galls on *Quercus cerris* are minute galls that are virtually unnoticeable as they barely protrude from the scales of the bud. In contrast, the agamic generation produces large conspicuous galls on either *Q. robur* or *Q. petreae* during the autumn months (Schönrogge et al. 2000). *Andricus quercuscalicis* is slightly different as the sexual generation induces small galls on the catkins of *Q. cerris* and the asexual generation produces a yellowish-green rigid gall on the acorns (knopper gall) of *Q. robur* in autumn, hence its common name of the knopper gall wasp (Schönrogge et al. 2000). The adults of the sexual generation are generally much smaller than the adults of the asexual generation, and produce fewer eggs, only 70–80 eggs in comparison to the 800–1000 eggs produced by the asexual generation (Hails and Crawley 1991).

The communities associated with these four *Andricus* species have been studied in detail (Stone and Sunnucks 1993; Rokas et al. 2003) and are fascinating in that the suite of natural enemies attracted to the sexual and asexual generations differ (Stone et al. 1995). It has been suggested that the alteration of generations in the Cyinipidae wasp may have allowed them to escape their natural enemies by “partitioning the host space” for the parasitoids (Stone et al. 1995). It is interesting that in general these four wasps share parasitoids and inquilines. For example, they share the parasitoids *Mesopolobus dubius* (except in *A. kollari*), *M. fuscipes* and *M. tibialis* (except in

A. corruptrix) in their sexual galls. However, there are parasitoids, for example, *Megastigmus stigmatizan,* which has currently only been seen to emerge from the agamic gall of *Andricus kollari* (Hayward and Stone 2005).

The appearance and structure of the gall is imperative in determining the community of insects (natural enemies) able to gain access to the gall. With regards to the *Andricus* wasps, the galls for each generation are noticeably different. The agamic galls have a longer developmental time (approximately four months), the size is almost 1000 times larger than the sexual galls, and they have thick woody walls and harbour inquilines and a more diverse community of parasitoids and inquilines (Stone et al. 1995). Conversely, the significantly smaller and thin walled sexual galls develop in approximately three weeks and do not appear to attract inquilines as effectively, thus attracting natural enemies that are predominantly parasitoids.

In addition to gall morphology, the host tree can also influence the parasitoid community. *Quercus robur,* which houses the agamic galls *of Andricus,* has been present in the invaded range for thousands of years and attracted other gall forming cynipids besides *Andricus,* indicating that there is already a rich diversity of parasitoids and inquilines present in the invaded range (Schönrogge et al. 2000). In contrast, *Q. cerris* has been invasive for fewer than 500 years, which has caused it to have a more patchy and random distribution (Stone and Sunnucks 1993; Stone et al. 1995). It is hypothesized that the more recent invasion of *Q. cerris* has likely affected the availability of parasitoids that are able to attack both the sexual and agamic galls as the sexual generation only develops on this host.

14.6.3 Leptocybe invasa (Fisher & LaSalle), Bluegum Chalcid (Eulophidae, Hymenoptera)

Leptocybe invasa, commonly referred to as the bluegum chalcid, is a wasp in the family Eulophidae that induces galls on *Eucalyptus* trees (Fig. 14.5). Although native to Australia, the first report, and subsequent description, of this insect was in 2000 when it was detected outside its native range, in Israel (Mendel et al. 2004). Subsequent to its detection in 2000, *L. invasa* has spread to Europe, Asia, Africa, South and North America, as well as New Zealand. By means of molecular markers it was shown that the global distribution of *L. invasa* in fact represents two different lineages, possibly different species (Nugnes et al. 2015). The lineage originally introduced into Israel (Lineage A) is also present in Europe, the Americas, eastern and southern Africa and parts of Asia, while Lineage B is present in Asia, Ghana and South Africa (Dittrich-Schröder et al. 2018). However, the exact distribution of these two lineages is only just being explored and is also expected to change over time due to the continued natural and human-assisted movement of the insect. Countries that contain both lineages could lead to genetic admixture (Dittrich-Schröder et al. 2018). Interestingly, to date (as of 2018), Lineage A, from which *L. invasa* was described, has not yet been found in Australia, the assumed native range.

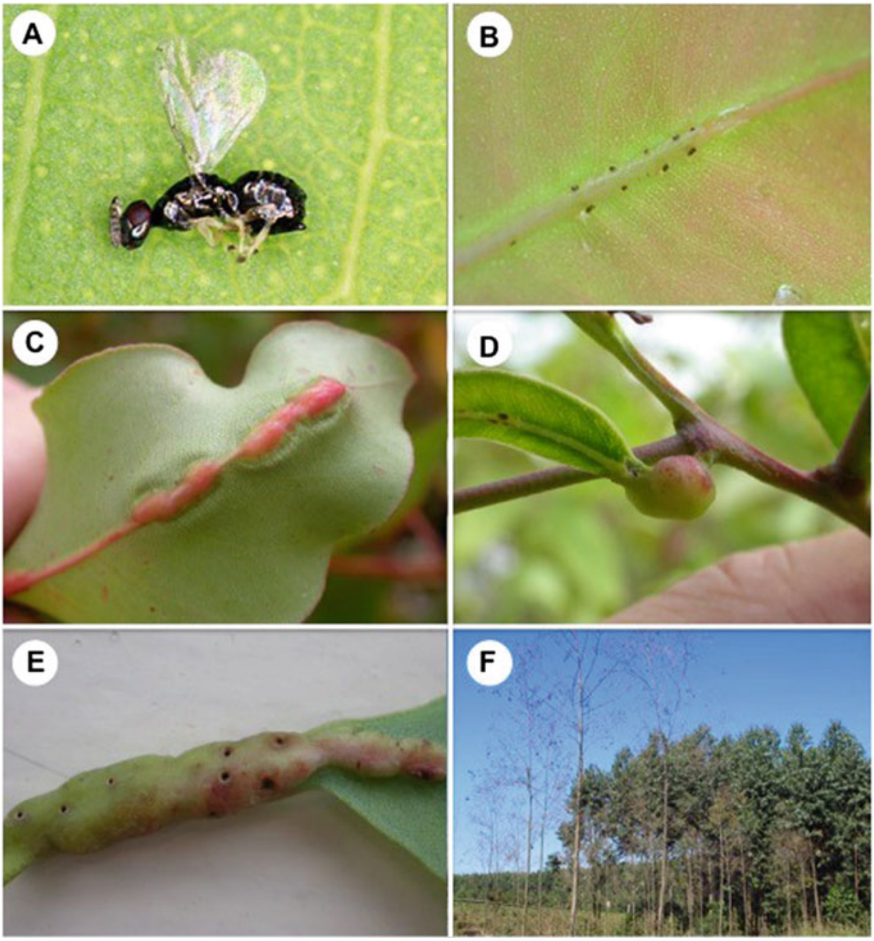

Fig. 14.5 The bluegum chalcid, *Leptocybe invasa.* **A** adult female wasp; **B** oviposition scars on midrib of leaf; **C** gall on midrib of leaf; **D** gall on petiole of leaf; **E** gall showing adult emergence holes; **F** damage from *L. invasa* (trees in foreground are a susceptible *Eucalyptus* clone, whereas trees in background are a resistant *Eucalyptus* clone)

Gall formation is induced when female *L. invasa* oviposits in the host plant. Oviposition sites include the stems, midribs and petioles of young leaves. Eggs are laid 0.3–0.5 mm apart in a line. A spherical ‘bump-shaped’ gall is formed and galls often fuse on a leaf (Fig. 14.5). Mendel et al. (2004) recognized five stages of galls, where the colour changes from green to pink to red as the gall matures, and light brown on adult emergence; however, the gall colour can also be influenced by exposure to the sun. The larvae develop within separate cavities within the gall. The exact number of larvae on one gall or leaf is highly variable, ranging from 1 to over 60 (Mendel et al. 2004).

Emerging adults are about 1.1–1.4 mm in length, although the male is often smaller in size. The head and body are brown with a blue to green metallic shine, and the legs are yellow (except last tarsal segment, which is brown) (Mendel et al. 2004) When *L. invasa* was first recorded in Israel no males were found in the population and the wasp was thought to reproduce thelytokously. However, males were subsequently found in Asia and other invaded areas, suggesting occasional sexual reproduction. Endosymbiotic bacteria in the genus *Rickettsia* are suggested to induce thelytokous parthenogenesis in *L. invasa* populations (Nugnes et al. 2015). Laboratory studies have stated a mean potential female fecundity of 158 eggs/female, and mean development time from oviposition to emergence of 132 days (at room temperature) (Mendel et al. 2004; Sangtongpraow et al. 2011).

Galling on the *Eucalyptus* hosts results in malformation and stunted growth of the plant and in severe cases tree death. In its invaded range, *L. invasa* has resulted in substantial losses in eucalypt plantations and is considered one of the most serious insect pests of *Eucalyptus*. One of the main management approaches is host selection; *L. invasa* has a relatively narrow host range, which allows more resistant species and hybrids to be selected for planting (Javaregowda and Prabhu 2010; Nyeko et al. 2010; Dittrich-Schröder et al. 2012). However, this approach requires the continual development of new species and clones due to the continual arrival of new insect pests with differing host preference. Biological control is the other main management approach. Biological agents released include *Quadrastichus mendeli*, *Selitrichodes kryceri*, *S. neseri* and *Megastigmus* species (Kim et al. 2008; Kelly et al. 2012; Dittrich-Schröder et al. 2014). There have also been a number of *Megastigmus* species which have been found to be associated with *L. invasa* in the invaded range (Sangtongpraow and Charernsom 2013); some of these are thought to be parasitoids of *L. invasa,* but in other cases, the role of these species and their interaction with introduced biological control agents is uncertain (Gevers et al. 2021). Systemic insecticides have been reported to be effective in some cases (Jhala et al. 2010), but their use is often limited due to high costs and restrictions from forestry certification bodies.

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