

XXIV SPRUCE APHID

(Elatobium abietinum Walker) (Hemiptera: Aphididae)Ann M Lynch^{1,2}¹ USDA Forest Service, Rocky Mountain Research Station, Tucson, Arizona, 85721, USA² Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona, 85721, USA

DESCRIPTION OF PEST

Taxonomy

Elatobium abietinum Walker is a spruce-feeding aphid that in Europe is referred to as the green spruce aphid (Day et al., 1998a) (Fig. 1). However, in North America *E. abietinum* is known simply as the spruce aphid, while the common name “green spruce aphid” refers to a different species, *Cinara fornacula* Hottes (Hemiptera: Aphididae) (<http://www.entsoc.org/common-names>). *Elatobium abietinum* is green-bodied with dull reddish eyes, 1–2 mm long (Johnson and Lyon, 1991; Koot, 1991), and it feeds on mature needles of dormant and nearly dormant spruce (*Picea*). Synonyms of *E. abietinum* include *Aphis abietina* Walker 1849, *Myzaphis abietina* Van der Goot 1913,



Figure 1 Close up of one spruce aphid, *Elatobium abietinum*. Donald Owen, California Department of Forestry and Fire Protection, University of Georgia, Bugwood.org.

Neomyzaphis abietina Theobald 1926, *E. abietinum* Börner 1930, and *Liosomaphis abietina* Börner & Schilder 1932 (Carter and Halldórsson, 1998).

Distribution

Population behavior, life cycle, and genetic diversity indicate that *E. abietinum* originated in continental Europe on Norway spruce (*Picea abies* [L.] Karst) (Carter and Halldórsson, 1998; Nicol et al., 1998; Halldórsson et al., 2004). It is also found in central Asia on *Picea schrenkiana* (Fischer et C.A. Meyer) (Ismukhambetov, 1976; Lynch, personal observations). The distribution of this aphid expanded rapidly in the 1800s and 1900s in the British Isles, France, Iceland, and New Zealand after the widespread planting of Sitka spruce (*Picea sitchensis* [Bong.] Carr.). It was well established in Western Europe by 1930. In North America, it was first reported in 1915 from Vancouver, British Columbia, and in 1916 from San Francisco, California (Essig, 1917; Swain, 1919). By 1927, spruce aphid was well distributed along the western coasts of the United States and Canada and became an important pest of Sitka spruce (Koot, 1991; Holsten et al., 2001; Schultz et al., 2009). It was found in the southwestern United States in 1976, where it exhibits extensive, severe outbreaks on Engelmann spruce (*Picea engelmannii* Parry ex. Engelmann) and blue spruce (*P. pungens* Engelmann) in montane ecosystems (Lynch, 2003, 2004). There are occasional reports of *E. abietinum* in Utah and Nevada (Hagle et al., 2003) and in eastern North America (Fedde, 1971, 1972; Carter and Halldórsson, 1998; Leaning, 2002). *Elatobium abietinum* now has an extensive global distribution, wherever spruce occur in areas with maritime climates (Carter and Halldórsson, 1998). Until

it was introduced to the southwestern United States, it caused significant economic damage only in areas with maritime climates, areas where the aphid, and often the tree, was exotic (Carter and Halldórson, 1998).

Damage

Type *Elatobium abietinum* aphids suck sap from needle phloem cells through needle stomata (von Scheller, 1963; Parry, 1971), causing stippling, chlorosis, and mortality of needles (Hussey, 1952; von Scheller, 1963; Fisher, 1987). Defoliation is the most noticeable symptom of attack (Fig. 2). A toxic substance may be injected into the needle with aphid saliva (Kloft and Ehrhardt, 1959; Parry, 1971; Fisher, 1987). If aphid population density is high for a prolonged period, extensive defoliation may occur (Day and McClean, 1991; Day et al., 1998a; Straw et al., 1998; Lynch, 2004). Defoliation reduces tree shoot growth, radial and height growth, and root mass, and severe defoliation may kill trees (Carter, 1977; Koot, 1991; Straw, 2001; Straw et al., 2002; Lynch, 2004).

Extent The extent of damage varies by region.

(1) Forests maritime locations *Elatobium abietinum* is considered to be one of the most serious pests of spruce plantations, especially in Britain, Iceland, and other

areas where Sitka spruce is grown commercially (Day and Leather, 1997; Nicol et al., 1998; Straw et al., 1998; Sigurdsson et al., 1999). Damage on the west coast of North America (from California to Alaska) is similar, with somewhat greater tree mortality, but commercial impact is less, because damage is mostly confined to coastal areas where Sitka spruce is not valued commercially (Koot, 1991; Holsten et al., 2001) (Fig. 3).

Straw et al. (1998, 2002) summarize the results of studies of losses to Sitka spruce in Britain, Ireland, Norway, and Iceland, including manipulative studies of pot-grown seedlings and of outplanted young trees, as well as natural aphid outbreaks in spruce plantations. *Elatobium abietinum* rarely kills trees in Europe, and its main effect is to reduce annual tree growth increments, though significant mortality does occur on Sitka spruce in New Zealand (Bevan, 1966; Nicol et al., 1998; Straw et al., 1998). Winter/spring aphid feeding before or at the time of shoot extension has an immediate effect on height growth, potentially for several years. Following defoliation, radial growth may be reduced for up to 7–8 years in older trees. The economic losses from the effects of aphids on plantation forestry are negligible if episodes are infrequent or not severe, but frequent and severe outbreaks can reduce cumulative diameter and stem volume growth 20–40% over a 50 year period (Randle and Ludlow, 1998).



Figure 2 Close view of damage of spruce aphid (*Elatobium abietinum*). Elizabeth Willhite, USDA Forest Service, Bugwood.org.



Figure 3 Spruce aphid (*Elatobium abietinum*) damage (brown discoloration) to stand of Sitka spruce. Andris Eglitis, USDA Forest Service, Bugwood.org

(2) Forests in European montane areas Damage from *E. abietinum* is seldom noticeable (Bejer-Petersen, 1962; Bevan, 1966; Carter and Halldórsson, 1998; Nicol et al., 1998; Halldórsson et al., 2004).

(3) High-elevation spruce forests of the southwestern United States Spruce aphid has become a chronic source of damage in this region, including occasional, very severe outbreaks (Lynch, 2003, 2004, 2009) on Engelmann spruce and blue spruce. Impact studies show that the degree of defoliation is much higher on Engelmann spruce than on blue spruce and more severe in the lower canopy (Lynch, 2004). Average mortality from a single aphid outbreak was 10% (Lynch, 2004), but reached 24–40% in severely defoliated trees and 70% in trees with severe pre-existing infection by western spruce dwarf mistletoe (*Arceuthobium microcarpum* [Engelmann] Hawksworth & Wiens) (Lynch, 2004, 2009). Mortality may continue for up to three years after defoliation (Lynch, 2004). Retention of foliage in the upper-third of crowns is critical for tree survivorship. Differences in tree defoliation and mortality in these studies were not associated with stand stocking, host abundance, tree age, or tree size (except that damage was greater to sub-canopy trees in multi-storied stands), or with elevation, aspect, or

slope steepness (Lynch, 2004, 2009). *Elatobium abietinum* is likely to significantly affect natural disturbance regimes and tree population dynamics in mixed-conifer and spruce-fir forests of the southwestern United States (Lynch, 2004, 2009). *Elatobium abietinum* has contributed to declines in habitat quality of the endangered Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis* J. A. Allen) (Koprowski et al., 2005).

(4) In Christmas tree plantings and urban areas *Elatobium abietinum* is a significant pest of spruce trees in maritime and montane environments, and of Sitka spruce in urban parks, because of the unsightly nature of aphid-caused defoliation and the sooty mold that grows on aphid honeydew (Cain, 1989; Koot, 1991; DeAngelis, 1994; Carter and Winter, 1998; Holsten et al., 2001; Hagle et al., 2003). Infestations are not usually detected until foliage is discolored, by which time it is too late to prevent aesthetic damage. Trees may not recover a full complement of foliage for five years (DeAngelis, 1994). *Elatobium abietinum* is also a pest of seed orchards, and appears to reduce seed and cone production seriously (Ruth et al., 1982; Sawchuck, 1994; Partridge and Borden, 1997), but effects have not been quantified. Effects on wildlife habitat are not documented.

Biology of Pest

General biology Von Scheller (1963) provides descriptions and drawings of the different life stages of *E. abietinum*. Spruce aphid feeds and develops on all species of *Picea*, with North American species being the most susceptible (Theobald, 1926; Nichols, 1987; Carter and Halldórsson, 1998). This aphid has no alternate host (Bejer-Petersen, 1962). Occasional reports of *E. abietinum* on fir (*Abies*), larch (*Larix*), Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), and pine (*Pinus*) probably either reflect accidental occurrences or non-persistent populations (Cunliffe, 1924; Dumbleton, 1932; Bejer-Petersen, 1962; Carter and Halldórson, 1998; Lynch, personal observation), or are actually the related species *Elatobium blackmani* Binazzi & Barbagallo (Blackman and Eastop, 1994).

Aphid biology and outbreak risk in coastal ecosystems of the North American Pacific Northwest are similar to what has been observed in Britain (Eglitis 1987, Koot 1991, Holsten et al. 2001). However, the life cycle, seasonal history, and damage are all quite different in inland montane ecosystems (Lynch, 2003, 2009).

The life cycle and biology of *E. abietinum* are described by von Scheller (1963) and Bevan (1966), including the holocyclic life history (which typically occurs in the aphid's native range), in which parthenogenetic reproduction is followed seasonally by sexual reproduction, which starts another annual cycle with the laying of winter eggs. In maritime areas, the species is anholocyclic (i.e., completely parthenogenetic), and it is on this form that most biology, impact, and control studies have been done. *Elatobium abietinum* has the capacity for rapid parthenogenetic population growth in spring or autumn, when foliage is dormant and temperature is favorable. In most maritime environments, this form of reproduction occurs in spring, but in Iceland and montane ecosystems of the southwestern United States, it occurs in autumn. In the colder areas of Europe and western Asia where *E. abietinum* is indigenous, the occasional outbreaks are minor and local (Bejer-Petersen, 1962; Bevan, 1966; Ismukhambetov, 1976; Carter and Halldórsson, 1998; Nicol et al., 1998; Halldórsson et al., 2004).

Elatobium abietinum sucks sap from needle phloem cells of the vascular bundles (Bevan, 1966). Old foliage is strongly preferred over new foliage, but new foliage becomes acceptable as it matures and trees enter dormancy. Population development and decline are

influenced primarily by temperature and the effects on aphid fecundity of seasonal variation in the levels of soluble nitrogen in needle sap (Parry, 1974; Day, 1984; Fisher and Dixon, 1986; Crute and Day, 1990; Dixon, 1998; Day et al., 2004). The nutritional quality of the food resource increases in autumn and decreases in spring as trees enter and exit dormancy, respectively, and aphid fertility is strongly associated with seasonal changes in amino acid concentration in needle sap (Day, 1984; Fisher and Dixon, 1986; Day et al., 2004). This effect is independent of crowding (Day et al., 2004). New foliage is nutritionally inadequate (Day et al., 2004) and chemically protected by terpenes in the epicuticular wax (Jackson and Dixon, 1966). Consequently, new foliage is not infested until it matures and dormancy is initiated (Bevan, 1966; Carter, 1977; Straw et al., 1998). Day et al. (2004) discuss the relative importance of density-dependent and density-independent factors that contribute to summer survival and spring and autumn population density changes. Usually, population development in autumn is limited by seasonal cooling (Hussey, 1952; Bejer-Petersen, 1962; Parry, 1979), except in Iceland and the southwestern United States (Halldórsson et al., 2004; Lynch, 2003, 2004, 2009). Sap quality can also determine whether or not aphids survive freezing temperatures in winter (Powell, 1974; Powell and Parry, 1976).

There is no summer aestivation (Parry, 1979). Low density of *E. abietinum* in summer coincides with low soluble nitrogen (Bevan, 1966; Parry, 1974, 1979; Carter, 1989), and summer survival is dependent on the ability of a few aphids of all instars to survive on nutritionally inadequate foliage, possibly due to higher fat reserves or the ability to feed on marginally superior trees or shoots (Parry, 1979). Many aphids in the summer generations fail to reproduce in summer (Parry, 1974; Day, 1984; Day et al., 2004).

Biology in maritime locations In areas with mild winters, including the North American Pacific Northwest (northern California to southeastern Alaska), *E. abietinum* is predominantly anholocyclic, overwintering as apterous parthenogenetic viviparae (female aphids that give birth to nymphs) (Parry, 1974; Carter and Halldórson, 1998). Alate viviparae sometimes are produced in spring and early summer (Hussey, 1952; Carter and Cole, 1977; Parry, 1973; Day, 1986) and occasionally in autumn (Hussey, 1952; Fisher and Dixon, 1986). When female alates are produced, they contribute significantly to rapid

population spread (Dumbleton, 1932; Halldórsson et al., 2004). Ovipares (sexual females that mate and lay eggs) and male alates are rarely observed in autumn (Fisher and Dixon, 1986; Harding and Carter, 1999; Carter and Halldórsson, 1998). Population density peaks in late spring or early summer and then collapses, primarily due to reduced fecundity as trees break dormancy, but also due to starvation, needle scarcity, loss of aphids on falling needles, emigration by alates, and the effects of parasitoids and predators (Hussey, 1952; Bevan, 1966; Parry, 1969a; Leather and Owuor, 1996).

Springtime outbreaks follow mild winters and early initiation of tree dormancy in the previous fall (Ohnesorge, 1961; Bejer-Petersen, 1962; Carter, 1972; Powell and Parry, 1976; Carter and Nichols, 1988) and can be terminated by late-season frost (Carter, 1972). Outbreaks occur in late winter and spring if the mean monthly temperatures of the preceding year remained above freezing and the minimum ambient temperatures remained above -7 to -14°C (Bejer-Petersen, 1962; Carter, 1972; Powell and Parry, 1976). Aphids are inactive at or below 6°C and may starve during prolonged cold periods (Powell and Parry, 1976). Overwintering survival is facilitated through accumulation of cryoprotectant chemicals in the haemocoel, but these chemicals vary seasonally and are lost in the spring (Parry, 1969b; Carter, 1972; Day and Kidd, 1998). Aphid mortality occurs when ice nucleation progresses from host needle tissue to feeding aphids or possibly from rime ice (Carter, 1972; Powell, 1974; Carter and Halldórsson, 1998). Outbreaks do not occur after every mild winter, due to the effects of predator and parasitoid populations (Crute and Day, 1990; Day and Kidd, 1998; Straw et al., 2009).

Sexual forms are rare in Great Britain (Hussey, 1952; Parry, 1973; Carter and Halldórsson, 1998). Though the life cycle is predominantly anholocyclic in maritime ecosystems, the occasional production of oviparae, male alates, and eggs in Britain, Denmark, and Norway (Fisher and Dixon, 1986; Carter and Austarå, 1994; Harding and Carter, 1997; Carter and Halldórsson, 1998) and evidence of gene flow among Great Britain, France, and Iceland (Halldórsson et al., 2004) indicate that parthenogenetic populations retain the capacity of a holocyclic life cycle.

The role of natural enemies in the dynamics of anholocyclic populations of *E. abietinum* has been the subject of controversy, particularly regarding the relative importance of host-plant nutrition (as discussed earlier)

and natural enemy regulation (Austarå et al., 1998; Day and Kidd, 1998; Day et al., 2004, and papers cited therein). Current evidence suggests that thermal conditions and seasonal changes in spruce needle sap nutrients are the primary factors influencing aphid population development and decline. However, in some circumstances natural enemies have the capacity to determine the amplitude of seasonal population fluctuation (Crute and Day, 1990; Leather and Owuor, 1996; Day and Kidd, 1998; Day et al., 2006; Straw et al., 2009), and such density-dependent effects can lead to population declines (Leather and Owuor, 1996; Austarå et al., 1998; Day and Kidd, 1998; Day et al., 2004; Straw et al., 2009). Straw et al. (2009) found that the abundance of generalist predators was more closely associated with the abundance of alternate prey than with *E. abietinum*. Outbreaks sometimes fail to occur after a mild winter, presumably because of predator and parasitoid population response to aphid populations the previous year (Crute and Day, 1990; Day and Kidd, 1998; Straw et al., 2009).

Population biology in Iceland is similar to that in Great Britain, except that populations develop in the autumn, with a minor peak in springtime (Austarå et al., 1997). Gene flow indicates that some sexual reproduction occurs (Halldórsson et al., 2004).

Biology in montane locations The life cycle and temperature relationships in North American montane ecosystems are presumably similar to those in colder continental European habitats, where *E. abietinum* is holocyclic, with population development and production of female apterae in spring and autumn, oviparae and male alates in autumn, and a cold-hardy overwintering egg (Kloft et al., 1961; Bejer-Petersen, 1962; von Scheller, 1963; Bevan, 1966). In high-elevation spruce-fir forests of Arizona, the life cycle includes parthenogenetic reproduction throughout the entire year when winters are mild, damaging populations in autumn and early winter, occasional damaging populations in spring, occasional female alatae in spring, and oviparae and male alatae in autumn (Lynch, 2003, 2009). The egg stage has not been confirmed in this region (Lynch, 2003).

Autumn populations of *E. abietinum* in the montane forests of the southwestern United States are more cold-hardy than populations in maritime Europe and the North American Pacific Northwest. Day and Kidd (1998) observed that *E. abietinum* reared in cool conditions

acquire greater cold hardiness. At 2400-3500 m elevation in Arizona, populations develop at temperatures below thresholds that prevent or diminish spring outbreaks in maritime ecosystems (Lynch, 2009). Aphids are typically active on warm, sunny autumn and early winter days, and aphids that survive nighttime temperatures and acute or prolonged cold events are able to reproduce (Lynch, 2009). Populations persisted in the Arizonan White Mountains after temperatures fell to -30°C in December 1990, with an extensive outbreak five years later (Lynch, 2009). Winter survival is probably ensured by the production of cold hardy eggs, though this stage has not been confirmed in Arizona. Likely explanations for greater cold hardiness in the montane ecosystem include acclimatization as a consequence of the cool and diurnally variable thermal conditions, genetic adaptation, and greater cold hardiness of Engelmann spruce, which would diminish the threshold at which ice nucleation begins in the needle.

ANALYSIS OF RELATED NATIVE INSECTS IN THE UNITED STATES

Native Insects Related to the Pest (Nontarget Species)

There are no other known species of *Elatobium* in the Western Hemisphere (Carter and Halldórsson, 1998). The biology and distribution of other *Elatobium* species are not well known, but they are native to China, Japan, Taiwan, eastern Siberia, Turkey, and Italy (Blackman and Eastop, 1994; Carter and Halldórsson, 1998).

Native Natural Enemies Affecting the Pest

No surveys or studies have been made of natural enemies of *E. abietinum* in North America. Generalist predators, such as green (*Chrysoperla*) and brown lacewings (*Hemerobius*) (both Neuroptera: Chrysopidae), coccinellid beetles, spiders, and syrphid flies are associated with *E. abietinum* infestations in Arizona (Lynch, personal observations). Some spiders are active predators all year on foliage in Arizona except in mid-winter during colder years. Infections by Entomophthorales fungi are also common in Alaska and Arizona. These predators and fungi do not appear to regulate *E. abietinum* populations in either spring or autumn, the main periods of aphid population increase.

HISTORY OF BIOLOGICAL CONTROL EFFORTS

Area of Origin of Insect

There are four known conifer-feeding species of *Elatobium*: *E. abietinum* on spruce (*Picea*), *E. blackmani* on true fir (*Abies*) in Italy and Turkey (and possibly more widespread), *Elatobium laricis* (Rupais) on *Larix sibirica* Ledebour in eastern Siberia, and *Elatobium momii* (Shinji) on *Abies firma* Siebold. & Zucc. in Japan (Blackman and Eastop, 1994; Carter and Halldórsson, 1998). Of these, only *E. abietinum* is known to exist in North America, where it is introduced. *Elatobium abietinum* is the only significant pest of the four. Population behavior, life cycle, and genetic diversity indicate that *E. abietinum* originated in continental Europe on Norway spruce (*P. abies*) (Carter and Halldórsson, 1998; Nicol et al., 1998; Halldórsson et al., 2004). It is found as a normally innocuous insect in Kazakhstan on *Picea schrenkiana* (Fisch. et May) (Ismukhambetov, 1976; Lynch, personal observations), and it might have a more extensive distribution in Asia than has been reported in the literature.

Areas Surveyed for Natural Enemies

Natural enemies of *E. abietinum* have been studied in Denmark, Great Britain, Iceland, Ireland, New Zealand, and Norway (Dumbleton, 1932; Austarå et al., 1997, 1998; Nielsen et al., 2000, 2001; Day et al., 2006; Straw et al., 2009), but surveys have not been conducted in North America. Von Scheller (1963) includes a brief report of natural enemies known from Germany.

Natural Enemies Found in the Native Range or other Invaded Areas outside USA

The influence of natural enemies in suppressing *E. abietinum* populations in maritime areas of Europe is not clear, but the overriding influences of climate and host nutrition (von Scheller, 1963; Parry, 1969b; Day and Kidd, 1998), and the aphid's seasonal avoidance of natural enemies suggests that the effectiveness of natural enemies is limited. Von Scheller (1963) indicates that parasitism rates are very low (1–2%) in Germany, the presumed native range of *E. abietinum*. Predators may be important in reducing aphid populations during the late summer and autumn in Europe, and in years following high populations (Crute and Day, 1990; Leather and Kidd, 1998).

Table 1 Known parasitoids and entomopathogenic fungal pathogens of *Elatobium abietinum*, compiled from von Scheller (1963), Austarå et al. (1997, 1998), Nielsen et al. (2001), and Nielsen and Wraight (2009).

Species	Collection Location
Hymenoptera: Aphidiidae <i>Lysaphidus schimitscheki</i> Starý <i>Praon</i> sp.	Germany, Great Britain, Norway Germany, Great Britain, Norway
Hymenoptera: Aphelinidae <i>Aphelinus abdominalis</i> (Dalman) <i>Aphelinus</i> sp.	Norway Germany
Hymenoptera: Pteromalidae <i>Asaphes suspensus</i> (Nees) <i>A. vulgaris</i> Walker <i>Coruna clavata</i> Walker	Norway Germany, Great Britain Norway
Entomophthorales: Ancylistaceae <i>Conidiobolus obscures</i> (Hall & Dunn) <i>C. coronatus</i> (Costantin) Batko	Great Britain Great Britain
Entomophthorales: Entomophthoraceae <i>Entomophthora planchoniana</i> Cornu <i>E. pyriformis</i> (Thoizon) Bälazy <i>Pandora neoaphidis</i> Remaudikre & Hennebert	Denmark, Iceland Iceland Denmark
Entomophthorales: Neozygitaceae <i>Neozygites fresenii</i> (Nowakowski) <i>Zoophthora phalloides</i> Batko	Great Britain, Denmark, Iceland, Norway Denmark

Elatobium abietinum is attacked by a wide range of invertebrate generalist predators, several species of parasitoids, and entomopathogenic fungi (Bejer-Peterson, 1962; von Scheller, 1963; Austarå et al., 1997, 1998; Nielsen et al., 2001; Day et al., 2006). These authors provide lists of parasites, predators, and entomopathogens associated with *E. abietinum* in different regions (Table 1, above). The most important of the generalist predators include green lacewings, brown lacewings, coccinellid beetles, spiders, harvestmen, syrphid flies, cantharid beetles, and elaterids. The relative importance of the different predators varies considerably between locations and years, but generally the lacewings and coccinellids seem to be the most common, followed by cantharids and syrphids.

Records of parasitoids are much less frequent than records of predators and parasitoids appear to be less effective, with parasitism rates rarely exceeding 10% (von Scheller, 1963; Parry, 1969; Austarå et al., 1998; Leather and Kidd, 1998). There appear to be few specialized parasitoids of this aphid (Blackman and Eastop, 1994; Austarå et al., 1997, 1998). Halme (1992) indicates that *Ephedrus kopezeni* Halme is specific to *E. abietinum* in Finland, but this parasitoid has not been found elsewhere (Austarå et al., 1997, 1998).

Entomophthorales fungi (Zygomycotina), particularly *Entomophthora planchoniana* Cornu, *Conidiobolus obscures*

(Hall & Dunn), *Conidiobolus osmodes* Dreschler, *Pandora neoaphidis* Remaudikre & Hennebert, and *Neozygites fresenii* (Nowakowski), are prevalent but sporadic and infect *E. abietinum* throughout its current distribution (Austarå et al., 1997; Nielsen et al., 2000).

Releases Made

Classical biological control of this aphid has not been attempted in North America, so no releases of natural enemies have been made. *Aphidecta oblitterata* (L.) (Coleoptera: Coccinellidae) was introduced to the North Sea island of Amrum, Germany, in 1966 for control of *E. abietinum* (Schneider, 1966), but effectiveness has not been reported (Leather and Kidd, 1998). *Hippodamia convergens* Guérin-Méneville (Coleoptera: Coccinellidae) and *Chrysopa* sp. (Neuroptera) were introduced to New Zealand in 1921 for biological control of various aphids, including *E. abietinum*, without success (Dumbleton, 1932).

RECOMMENDATIONS FOR FURTHER WORK

Sitka spruce in coastal environments and Engelmann spruce in montane ecosystems are being affected by both *E. abietinum* and climate change, which could reduce their

presence in future forests (Lynch, 2004, 2009). Population growth by *E. abietinum* in late autumn and early winter and in early spring is an effective strategy to avoid parasitoids and predators (Bejer-Petersen, 1962; Parry, 1969b), and that phenology reduces the potential for successful biological control of this species. Also, the low commercial value of these spruce in North America makes substantial investment in management and biological control of *E. abietinum* or in the development of resistant host varieties uneconomical. Should these circumstances change, development of resistant varieties is likely to be a useful approach to management (Day et al., 1998b; Lewis et al., 1999; Harding et al., 2003) and would be facilitated by identification of, and seed collection from, resistant trees.

Surveys should be conducted to identify native North American natural enemies of *E. abietinum*. Further research is also needed to better understand the effects of predators and entomopathogens on population dynamics of *E. abietinum*, especially on the effects of summer- and autumn-active agents on moderating aphid population density the following year. Surveys and collections of natural enemies in continental Europe and western and central Asia should focus on autumn-active agents and should be conducted in warm, dry years, when *E. abietinum* is more likely to be at higher densities. Further research is also needed on the ecological requirements of potential biological control agents in maritime and cold ecosystems.

Because the seasonality of *E. abietinum* population growth (in autumn and early spring) limits the influence of parasitoids and predaceous insects on this aphid, and because the most effective known predators are generalists requiring alternate prey, it may be useful to study the entomophthoralean fungi associated with this aphid. Fungal pathogens known from *E. abietinum* include species of *Batkoa*, *Conidiobolus*, *Entomophaga*, *Entomophthora*, *Neozygites*, *Pandora* (= *Erynia*), and *Zoophthora* (Latgé and Papierok, 1988; Humber, 1989, 1992; Balazy, 1993; Nielsen et al., 2000; Keller, 2006; Nielsen and Wraight, 2009). With few exceptions, host ranges of the species reported from spruce aphid are restricted to the Aphididae (Keller, 2006; Nielsen and Wraight, 2009). Despite taxonomic diversity, the different species exhibit similar life cycles and ecology with rapid sporulation and infection, traits that facilitate exploitation of short windows of favorable environmental conditions and rapid spread within host populations (Pell et al., 2001; Nielsen and Wraight, 2009). Transmission of entomophthoralean fungi is possible

between different aphid host species, and other aphid species may serve as reservoirs for entomophthorales when *E. abietinum* is scarce (Nielsen et al., 2001). Additional studies are needed to determine the natural occurrence, diversity, environmental requirements, and pathogenicity of entomophthoralean fungi in different areas infested by *E. abietinum*. These studies might identify candidates for release in new areas. Entomophorales have had some success as biological control agents (Pell et al., 2001). Release of *Zoophthora radicans* (Brefeld) Batko contributed to the decline of the spotted alfalfa aphid (*Therioaphis trifolii* f. *maculata* [Buckton]) (Hemiptera: Aphididae) as a pest in Australia, although biological control is primarily attributed to the parasitoid *Trioxys complanatus* Quilis (Hymenoptera: Braconidae) (Hughes et al., 1987; Pell et al., 2001). Releases of *Neozygites fresenii* (Nowakowski) Batko against cotton aphid (*Aphis gossypii* Glover) (Hemiptera: Aphididae) in California and *Entomophaga grylli* (Fresenius) Batko against grasshoppers (Orthoptera: Acrididae) in Australia had some success (Pell et al., 2001; Steinkraus et al., 2002), but long-term effectiveness was not determined. The sporadic nature of entomophthorales epidemics in high density aphid populations suggests that they may require specific environmental conditions. Still, in North America the overriding objective of biological control is likely to be conservation of *Picea* spp., so biological control measures that moderate the most severe outbreaks would probably be sufficient.

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