Forestry Commission

The Green Spruce Aphid in Western Europe:

Ecology, Status, Impacts and Prospects for Management

Edited by
Keith R. Day, Gudmundur Halldórsson,
Susanne Harding and Nigel A. Straw

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The Green Spruce Aphid in Western Europe: Ecology, Status, Impacts and Prospects for Management

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Front Cover: The green spruce aphid *Elatobium abietinum.* (Photo: G. Halldórsson)

Back Cover: Distribution of the green spruce aphid.

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Preface

The intensification of the European forest industry has been relatively recent in the time-scale of forest growth, and many of the longer-term economic and environmental consequences of new developments are unknown. Above all, the European Union is challenged by the need to set in place an enlarged but sustainable development programme for its forests; a programme which delivers high quality forest products at low cost, and one which addresses fundamental questions of environmental sustainability. The challenge is particularly acute for Sitka spruce, an exotic species, and for some other spruces which are the mainstay of the forest development programme in a large part of the European Union. Sitka spruce is one of the predominant plantation species in north western maritime areas of the EC where it outperforms other species with a high timber yield (9-15 m^3 ha^{-1} yr^{-1} stemwood). It is therefore already one of the most productive trees in Europe and progressive genetic gains are enhancing this reputation. However, it is a species with some major pest problems which demand environmentally sensitive management.

Tree breeding programmes in Denmark and Great Britain have improved potential productivity of Sitka spruce but protection of these new genetically-defined trees needs careful consideration if widespread pest problems are to be avoided in future. The most ubiquitous and most generally debilitating pest of spruces in the maritime regions of western Europe is the green spruce aphid, *Elatobium abietinum*. The aphid partially defoliates but rarely kills spruce, and until recently the sub-lethal effect of large aphid populations on the growth and productivity of individual trees and of whole forests has been largely unknown. Coupled with this, the effects of silviculture and natural enemies on the green spruce aphid are also poorly understood. Are there ways in which the growth of aphid populations could be further constrained by natural enemies and can resistant trees be defined and given greater prominence in tree breeding programmes ?

These questions, and others connected with the development and regulation of green spruce aphid pest problems in Europe, were the subject of a European Community Concerted Action funded in part by the EC Agriculture, Fisheries, Forestry and Agro-Industry Specific Programme as project AIR3-CT94-1883. This volume is the product of a collaboration between forest research institutes in the four European states that participated in the Concerted Action, and a number of other contributors whose work is highly relevant to the project. It provides a comprehensive summary of current knowledge of the green spruce aphid as a pest of spruce and suggests what additional information is required to implement a pest management programme. It is the aim of this project, in due course, to provide foresters and forest managers with simple and practical options in the choice of plant material for forest development, and measures associated with its cultivation that will best protect it from the threat of aphid pest problems throughout the life of the crop.

Chapter 1

Origins and background to the green spruce aphid in Europe

Clive Carter and Gudmundur Halldórsson

Summary

An account is given of the original records of *Aphis abietina* (syn. *Elatobium abietinum*) in the British Isles and the defoliation damage that it caused to its spruce host plants. *E. abietinum* becomes a pest problem in areas having a mild winter climate where the aphid is anholocyclic; this situation is particularly prevalent in those areas of northwestern Europe that have a maritime climate.

In Asia, two other known species of *Elatobium* occur on conifers, and there have been five other species described from non-conifer hosts, but opinion is that these could be more appropriately placed in other aphid genera.

From its original description in Europe, *E. abietinum* has now been found to be extending into several more distant parts of the world where plantations of spruce have been established. Aphid attacks in plantation forestry in northwestern Europe (Britain, France and Iceland) can be documented particularly in those areas where spruce is not indigenous.

Earliest records of the green spruce aphid and damage caused

It may be ecologically significant that the green spruce aphid was first described and recorded as a troublesome pest in a part of Europe where its host plant, spruce, was growing as an exotic species. *Aphis abietina* was among the first of many aphid species collected in north London by Francis Walker who made important contributions to aphidological knowledge in the period 1840-1860 while employed at the British Museum in London (Doncaster, 1961).

When George Buckton wrote his four volume *Monograph of the British Aphids* he said for *Aphis abietina* "Found pretty numerously at Wanstead [N.E. London] on the spruce-fir" (Buckton, 1879). He goes on to say that "This insect does not appear in the lists of Kaltenbach [Germany], Koch [Germany], or Passerini [Italy]" who were all recording aphids in the mid nineteenth century. Furthermore, nothing appears to resemble the green spruce aphid amongst Linnaeus's species, even though spruce trees are widespread over Sweden.

Theobald's (1914) graphic account of serious defoliation damage to spruce include the first of many records of this aphid occurring in Ireland (Carter *et al.*, 1987). Theobald (1926) also found "no reference to this spruce aphis on the Continent, but... remember finding it near Odde in [West] Norway in 1892".

Original description of the green spruce aphid

The original description of *Aphis abietina* by Walker (1949) and the detailed figures of the lectotype in the collection of the Hope Department of Entomology, Oxford, drawn by Doncaster (1961) leave little doubt that this is the same species namely *Elatobium abietinum* (Walker). The label on the slide has the collection data 'Spruce fir. Southgate May 6-48'. At this time *Picea abies* was known in Britain as spruce fir or Norway spruce fir by the Latin binomials as *Pinus abies,* and *Abies excelsa* at a later date. It would seem reasonable to assume that Walker's specimens were from a planted specimen tree of what we know today as *Picea abies* (L.) Karst.

Synonyms of the green spruce aphid

At the time Walker was describing the green spruce aphid, both this and many other aphid species were assigned to the genus *Aphis*. Doncaster (1961) gives a comprehensive list of synonyms and their references. The main synonyms, authors and dates are summarised as follows:

Aphis abietina	Walker, 1849
Myzaphis abietina	Van der Goot, 1913
Neomyzaphis abietina	Theobald, 1926
Elatobium abietinum	Börner, 1930
Liosomaphis abietina	Börner & Schilder, 1932

After Theobald (1926) proposed the new generic name *Neomyzaphis* in his detailed description for this species, the combination *Neomyzaphis abietina* remained in popular usage in accounts of this pest for many years (Dumbleton, 1932; Chrystal, 1937; Fox-Wilson, 1948; Hanson, 1952; Crooke and Bevan, 1960 and Bejer-Petersen, 1962). The generic name *Elatobium* of Mordvilko (1914) largely remained unused in British forestry literature until after 1960 following the publication of works by Cottier (1953), Doncaster (1961) and Eastop (1966).

Host plants of the green spruce aphid

Field collections from plantation forests and arboreta have shown that *E. abietinum* can develop to a varying degree on all species of *Picea* in cultivation. Theobald (1926) lists 14 species of *Picea* as foodplants and recognised from observations at Kew that European and Asiatic species were damaged much less with the exception of Norway spruce, which was seriously injured. The North American species *P. sitchensis, P. pungens, P. engelmanni* and *P. alba (= P. glauca)* are recorded as being seriously damaged, and he gives a number of observations on interspecific variation on needle discoloration and/or defoliation following *E. abietinum* attack.

Experimental comparisons of aphid performance on 20 different spruce species have been made by Nichols (1987). She similarly found greater susceptibility within the North American range of species; but there was great variation in the Asiatic species, in particular *P. glehnii* and *P. brachytyla* showed resistance, whereas *P. asperata* and *P. jezoensis* supported rapid aphid growth and development of colonies. It appears from further studies that secondary plant compounds, in particular certain volatile terpene compounds in the resistant species have a deterrent effect on aphid feeding (Nichols, 1988). These unfavourable volatile compounds are also present with the leaf waxes of young spruce foliage making the youngest needles resistant to *E. abietinum* in the early summer (Jackson and Dixon, 1996).

The green spruce aphid is an oddity in the subfamily Aphidinae by feeding on spruce (a conifer) rather than higher plants, and unlike many other aphids that flourish on actively growing nutrient-rich foliage, this species is quite unable to take advantage of this food resource preferring instead mature needles.

Although there have been records of *E. abietinum* making small insignificant ephemeral colonies on plants in other conifer genera, e.g. *Larix sibirica* (Volkova, 1970), there are other host genera records that have also arisen, perhaps due to confusion in botanical genera.

Other *Elatobium* species and their host plants

In their book on *Aphids on the world's trees* Blackman and Eastop (1994) list five species in the genus *Elatobium* and comment that the genus includes a biologically diverse group of species. Miyazaki (1971) includes species with other host plants that occur in Japan and suggests that those species that do not have conifers as their host plants are distinct from the conifer feeding species at the subgeneric level and could be assigned to the genera *Ericolophium* and *Neoacyrthosiphon.* The list of currently used names, host plants and distribution are summarised in Table 1.1.

Another species, *Aphis indecisa* Walker, 1849, recorded from *Juniperus communis* was placed in the genus *Liosomaphis (Elatobium)* by Börner and Heinze (1957). According to Doncaster (1961),"no material of Walker's *indecisa* exists. The description seems to refer to the apterous form of the aphid described as *incerta,* which is probably *Aulacorthum solani* (Kaltenbach)", a polyphagous species.

Table 1.1

Species with conifer host plants	Host	Distribution
Elatobium abietinum (Walker, 1849)	*Picea* spp.	Europe, but see map (Figure 1.1)
Elatobium momii (Shinji, 1922) syn. *momifoliae* Sinji, 1924 syn. *abietifoliae* Shinji, 1924 syn. *piceana* Inouye, 1939	*Picea jezoensis* and *Abies firma*	Japan
Elatobium laricis (Rupais, 1974)	*Larix sibirica*	Eastern Siberia
Species with non-conifer host plants		
Elatobium hidaense (Takahashi, 1961)	*Salix* sp.	Japan, Kamschatica
Elatobium salicifoliae Zhang, 1985	*Salix* sp.	China
Elatobium trochodendri Takahashi, 1960	*Trichodendron aralioides*	Japan
Elatobium itoe (Takahashi, 1925)	*Rhododendron reticulatum*	Japan, Taiwan
Elatobium taisetsusanum Miyazaki, 1971	Umbelliferae	Hokkaido

Distribution of the green spruce aphid

World distribution

The first distribution map of *Elatobium abietinum* published by the Commonwealth Institute of Entomology in 1966 with a list of countries in which the pest was known to occur shows the British Isles, northern France, Denmark, Germany, Switzerland and Austria as the largest continuous area of its distribution in Europe. Small areas of Norway, Sweden, Finland, Latvia and Iceland are also shown. There was only a limited distribution recorded for North America; in New Zealand throughout both North and South Islands and Tasmania where it was also recorded. A revised map (CAB International, 1986) shows an extended distribution, particularly in North America and a single record for South America in Chile. Further records of world distribution have been added to this map (Figure 1.1) including that for the Falkland Islands (Low, 1986).

European distribution

From early accounts, notably that of Theobald (1926), it was quite apparent that *E. abietinum* was widespread throughout the British Isles, but in Scandinavia it had a more patchy distribution (Ossiannilson, 1959; Ø. Austarå, private communication). Published records and recent collections from different provinces for

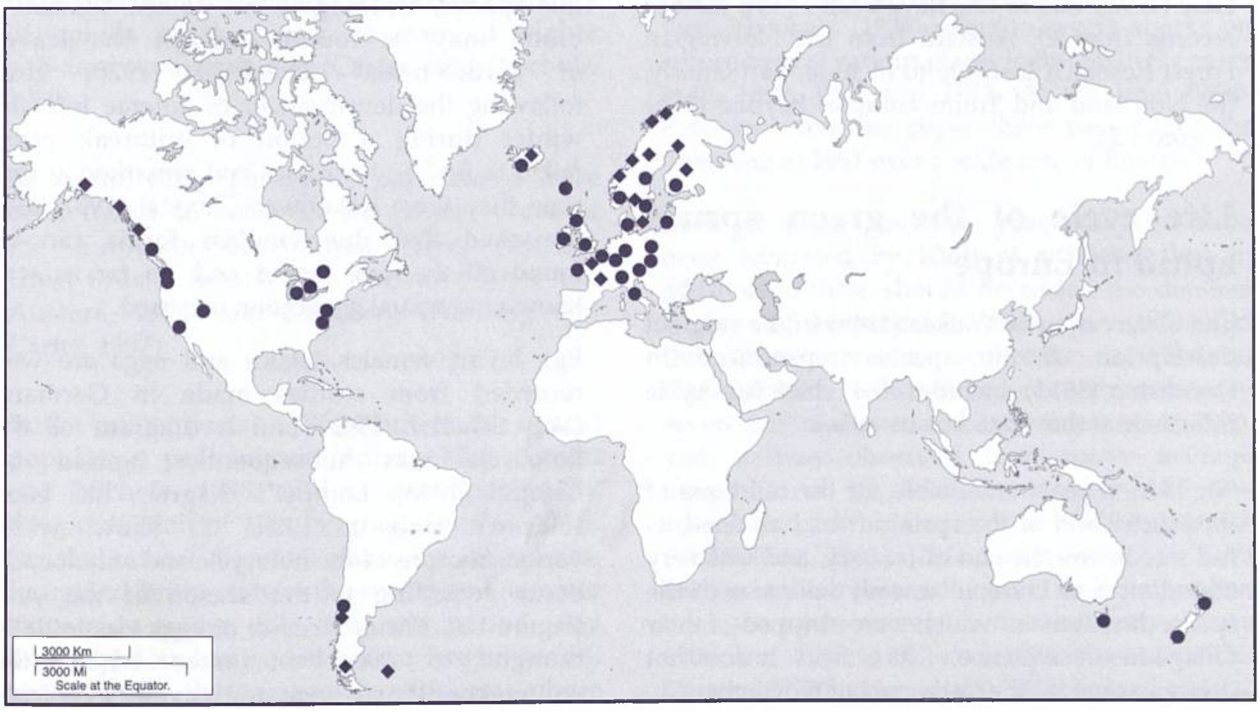

Figure 1.1 World distribution of the green spruce aphid *Elatobium abietinum* (Walker). Map redrawn from CAB International Pest Distribution Map 222 (1986); records to 1986 with the symbol ●; recent records from the authors added with the symbol ◆.

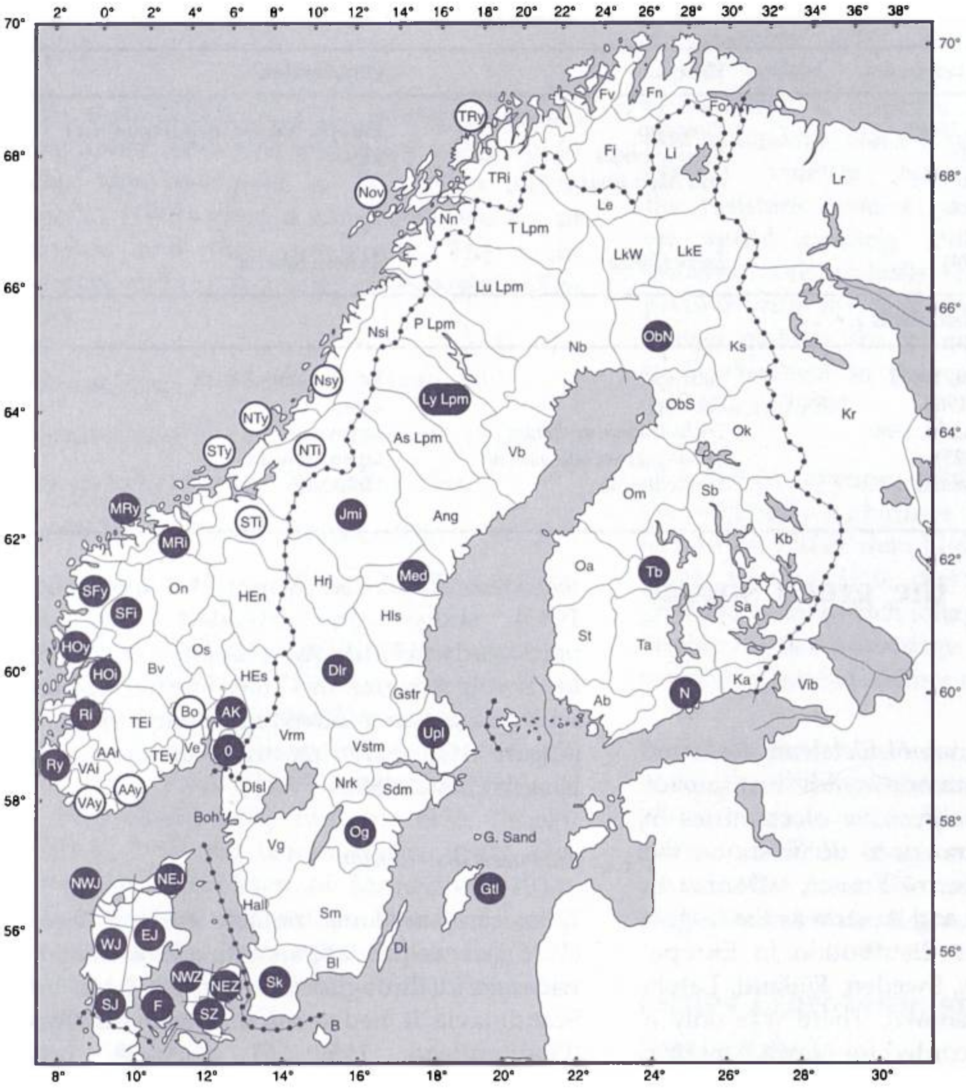

Figure 1.2 Distribution of county or province records of the green spruce aphid *Elatobium abietinum* (Walker) in Fennoscandia and Denmark. Map redrawn from Heie (1992) with his records added with the symbol ●; other records from Norway (Ø. Austarå) with the symbol ○.

Fennoscandia and Denmark were assembled by Heie (1992), and to this have been added further records from Ø. Austarå from the Norwegian Forest Research Institute to include, particularly, the Nordland and Troms counties beyond 68°N (Figure 1.2).

Life cycle of the green spruce aphid in Europe

The observation of Walker (1849) in the original description of the species reproduced in Doncaster (1961) includes the chief life cycle information that concerns us today.

"In 1846, a year remarkable for the mildness of the winter and of the spring, it had attained its full size before the end of January, and was very abundant near London beneath the leaves of the spruce-firs, some of which were stripped of their foliage in consequence of its attacks. It does not disappear before the latter part of November."

Gillanders (1908) also records that "During the winter months the apterous females of this species, which give rise to the summer's brood may be found amongst the leaves of spruce-trees." Theobald (1926) after following the development of apterae into the winter during a period of outbreak years failed to find any sexuales and remarked at that time they were unknown; Chrystal (1937) also remarked that the wingless forms can be found all the year round and, so far as was known, no sexual generation occurred.

Egg laying females, males and eggs are well recorded from studies made in Germany (Von Scheller, 1963) and a diagram of the holocycle was subsequently figured by Lampel (1968). Lampel's diagram has been re-drawn and modified to show when various morphs of the holocycle and anholocycle occur according to the season of the year (Figure 1.3). The occurrence of eggs was initially thought to occur in areas where the winter conditions were too severe to enable apterae to survive. Prolonged periods during the winter months with low temperatures

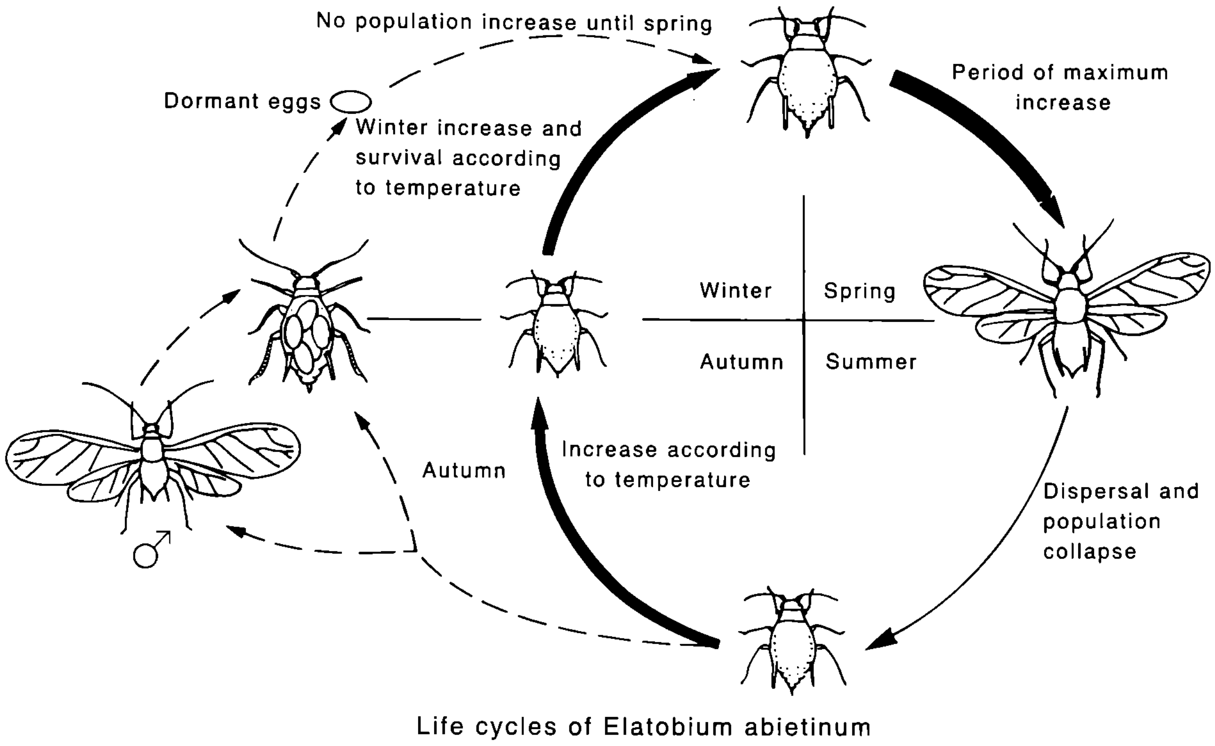

Figure 1.3 Life cycle of *Elatobium abietinum* (Walker). Spruce is the only true host plant for this aphid species. The continuous line with arrows denotes the anholocycle, being the most usual style in oceanic climates of Europe. The broken line denotes the forms also found in the complete holocycle. Paracyclic populations include a mixture of successful overwintering forms. The thicker the lines the more populous are the colonies.

were shown to prevent potential outbreaks in the early spring (Bejer-Petersen, 1962). Carter (1972) later showed that significant mortality occurs when air temperatures fall below -8°C. However, air humidity is also influential; freezing fog droplets causing the growth of rime ice-crystals markedly increases mortality of aphids at the same or even at higher sub-zero temperatures (Carter and Nichols, 1989).

In recent years paracyclic populations have been found to occur in the milder areas of the European distribution. These include Great Britain, Ireland and Norway (Carter and Austarå, 1994) and Denmark (Harding and Carter, 1997).

In the milder parts of Great Britain the annual population peak occurs during May (Carter and Nichols, 1988) and is accompanied by the production of alate migrant females which are the natural dispersal phase for the species. In upland Britain where the spring and summer climate is cooler, this dispersal period may be delayed and extended over a longer period, but even in these areas the dispersal phase is essentially finished by August (Carter and Cole, 1977).

Outbreak years of the green spruce aphid

The frequency and possible explanation of peak years of attack on Sitka spruce in north-west Europe has been analysed by Bejer-Petersen (1962) from the year 1920 to 1961. But even before then, Theobald (1926) refers to severe attacks on spruce trees at various places in Britain in the years 1846, 1899, 1906 and 1913. At the time Bejer-Petersen wrote his paper there were outbreaks occurring in 1961 over a wide area of Europe.

Most of these previous year's attacks have been tabulated by Kloft *et al.* (1961) but in addition to these should be added the detailed survey of Switzerland by Maksymov (1961) and the more recent outbreak in Poland (Szelegiewiez, 1975). A second extraordinarily severe outbreak occurred in Switzerland in 1980, and it was observed that above average temperatures in several successive winters contributed towards causing the 1980 outbreak (Maksymov, 1981). This appears also to have been a similar pattern in parts of Britain when there were two successive mild winters, namely 1966 and 1967, 1970 and 1971 (Carter, 1972a; Carter, 1972b) and probably 1979 as well as 1980 for certain pockets of Sitka spruce growing in South Wales (Carter and Nichols, 1988).

Spread of the green spruce aphid with plantation forestry in northwestern Europe

Elatobium abietinum has probably been present for some time in Scandinavia and other parts of northwestern Europe where long established *P. abies* forests occur. However, in other parts of Europe where *P. sitchensis* has recently been introduced, the conspicuous damage by the aphid has been readily detectable and its spread has therefore been noted. The following centres are worthy of mention.

The British Isles

For many geographically isolated parts of Europe, notably the British Isles and Iceland, there are no native spruce trees. Although *Picea abies* is thought to have been cultivated in Britain from the year 1548 (Morse, 1959) and *P. sitchensis* from 1832, it was not until the two post-war decades 1945 to 1965 that really extensive afforestation with these productive species had taken place, thus increasing the spruce plantation area in England alone by $2^{1}/_{2}$ times to 90 000 ha, representing 10% of the total forest and woodland areas (Carter, 1983). Most of the new spruce plantations were on non-forest land, such as exposed hill farms or moors, so the forest ecosystem was from the start very imbalanced. It is plausible that this had resulted in the many outbreaks experienced in afforested areas of Scotland and Ireland.

Records of *E. abietinum* distribution in Britain by the time Theobald (1926) wrote his account suggest that the aphid was already well distributed over much of the British Isles, so infestation of these new plantations would be only a matter of time The raising of planting stock in areas where infestation of the young trees can readily take place and then transporting these to remote planting sites, has no doubt accelerated the spread of this aphid in the British Isles, and the same circumstances probably apply to other countries.

France

Between 1950 and 1960 there was an increase in the planting of *P. sitchensis*, particularly on the Channel coastal areas of Brittany as a result of successful timber production in Britain being reported (Leroy and Malphettes, 1969). However, the widespread outbreak of *E. abietinum* in 1961 that affected much of Europe extended into these young plantations in both Brittany and Normandy (Joly, 1961). As is the case in the

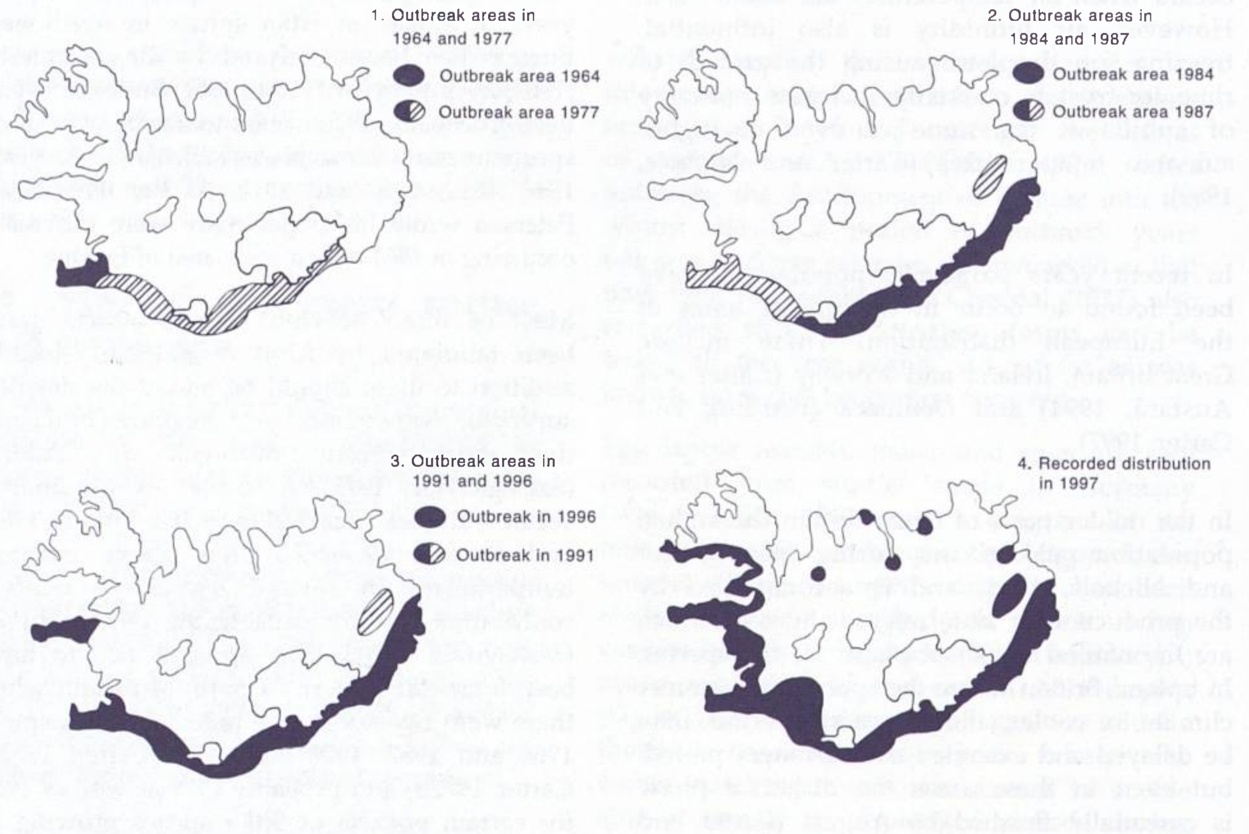

Figure 1.4 The spread of *Elatobium abietinum* into new areas of Iceland since its original recorded occurrence in Reykjavik in 1959.

British Isles, the aphid overwinters as apterous virginoparae, and severe outbreaks appear to be more damaging on poor shallow soils (Carter and Nichols, 1988; Leroy and Malphettes, 1969).

Since the early plantings in western France, the area of *P. sitchensis* is now in excess of 30 000 ha and the majority of the plantations between 20 and 30 years old. These extend to the Millevache plateau down to 45°N in the Limousin.

The aphid is well distributed in these areas but outbreaks in 1987 and 1988 are only recorded from Britanny in the past 10 years (Lempérière, personal communication). These outbreaks occur on poor sites, mostly 30 to 35 year old stands, but all age classes are affected by the aphid. In the Limousin, the last outbreak was recorded in 1994 near Limoges between 500 and 600 m altitude.

Iceland

The green spruce aphid was first recorded in Iceland in November 1959, in a nursery in Reykjavik. At that time this nursery was used for storing imported Christmas trees. Attempts to eradicate the aphids failed and it was found in several gardens in Reykjavik in late summer and autumn of 1960 (Bjarnason, 1961; Ragnarsson, 1962). The first major outbreak was in southwest Iceland in 1964. After that five major outbreaks have followed; in 1977, 1984, 1987, 1991 and 1996 (Ottósson, 1985; Blöndal, 1988; Halldórsson, unpublished data) and *Elatobium* has now been recorded in all parts of the country (Figure 1.4).

All outbreaks have been in the late summer/autumn/early winter period, and outbreaks have never occurred after severe winters (Halldórsson, 1995). These outbreaks have covered all the distribution area at each time, except the outbreak in 1984 and in 1996. The outbreak in 1984 was heaviest in the eastern fjords, but milder attacks reached west to the mid south coast (Figure 1.4, 2). No outbreaks occurred in the distribution area west of that (Ottósson, 1985). The lowest minimum temperature in winter of 1983-84 in the area of heavy outbreak was -9.8°C to -12.2°C. The lowest minimum temperature in the area with mild outbreak was -11.6°C to -11.9°C. The lowest minimum temperature in non-outbreak areas of the distribution area was -12.1°C to -16.5°C. The lowest minimum temperature in areas neighbouring the distribution area was -12.8°C to -20.6°C. The outbreak in 1996 was in the coastal areas from west Iceland to the eastern fjords. No outbreaks occurred in inland areas or in north Iceland (Figure 1.4, 3). This distribution of attacks coincides with the severity of frosts in December 1995 (Halldórsson, unpublished data). Studies of freezing tolerance of *Elatobium* in Iceland have shown that no mortality is found at temperatures above -12°C and the LT50 value is *c.* -15°C (Halldórsson, 1995).

The development of the green spruce aphid in Iceland seems to be exclusively parthenogenetic, since males or eggs have never been found. Alates are encountered at different times of the year, but they are always a very low proportion of the population. Genetic studies on the green spruce aphid indicate that the Icelandic population is divided into two different genetic lineages, one has hitherto only been found in the western part of the distribution area, and the other only in the eastern part. No overlapping between lineages has been found (Sigurdsson *et al.*, unpublished).

Concluding remarks on the origin of the pest problem and distribution

It would appear that the combination of a susceptible host plant, Sitka spruce, growing in areas with oceanic climates and mild winters has enabled *E. abietinum* to breed freely and cause significant foliage damage and subsequent growth losses. Under these set of circumstances, many of the forests that are attacked may have, as yet, an impoverished or ill adapted forest ecosystem which fails effectively to reduce the increases of this pest.

Along the west coast of North America *E. abietinum* has been recorded as damaging *P. sitchensis* for some time (Holms and Ruth, 1968) and is now known throughout the coastal range from Alaska to California. Since 1960 there have been infestations along most coastal areas of Queen Charlotte Islands and between 1981-1991 there has been significant damage to both natural spruce forests and ornamental trees in coastal regions of British Columbia (Koot, 1991). It appears strange, however, that there are no major reports of aphid attack in the Sitka spruce range before 1960, unless some ecological changes have occurred. Such sudden outbreaks show similarities with other introductions of new unregulated forest pests.

The many distribution records of *E. abietinum* throughout Europe, and the existence of holocyclic populations there suggest that it was originally associated with *Picea abies* rather than

P. sitchensis (Bejer-Petersen, 1962). This is supported by the fact that *P. abies* and other Palaearctic species show less reaction to the aphid's feeding than does *P. sitchensis* and other nearctic species all but one. The other aphid species assigned to the genus *Elatobium* are all from Asia (see Table 1.1). It is also in Eastern Asia that speciation of the genus *Picea* appears to have taken place (Wright, 1955). Possible exposure to an *Elatobium* species in this region may be the reason why the most highly resistant *Picea* species occur there.

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Plate 1 Green spruce aphid, *Elatobium abietinum* (Walker). Adult aptera.

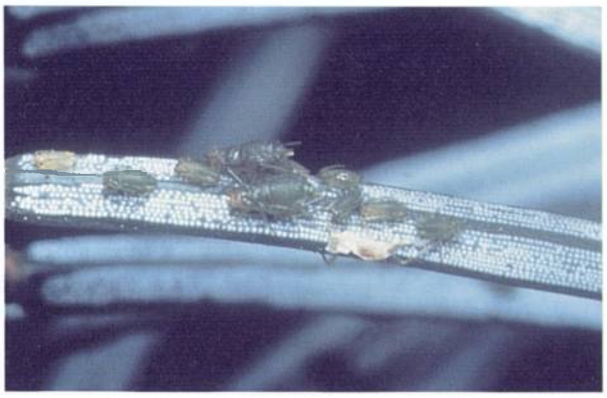


Plate 2 *E. abietinum*. Adult and nymph apterae on Sitka spruce.

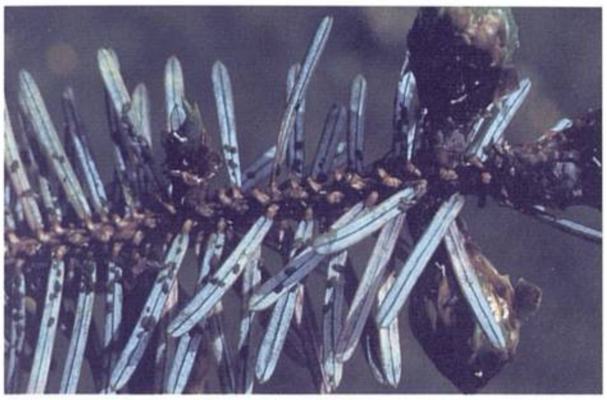


Plate 3 Spring infestation of *E. abietinum*. Aphids occur mainly on the underside of the needles. *(S. Harding)*

Plate 4 Sitka spruce showing the yellowing of older needles characteristic of attack by *E. abietinum*. Yellow needles die and fall from the shoot within a few weeks.

Plate 5 Damaged older needles and healthy current shoots typical of spring infestation by *E. abietinum*. Norway spruce at Windsor, UK, in June 1971.

Plate 6 Complete loss of older needles from young Sitka spruce following severe infestation. Black sooty moulds, which thrive on honey-dew excreted by the aphids, coat the lower stem and main branches. Thornthwaite Forest, UK, May 1971.

Plate 7 Defoliation of 5-year-old Sitka spruce following autumn infestation. Needle loss is concentrated in the upper canopy. Banteer, Ireland, January 1973.

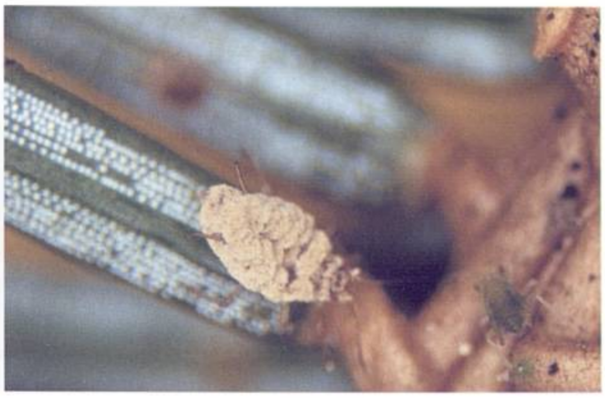
Plate 8 The tree in Plate 7 photographed in May 1973.

Plate 9 Needle browning in Sitka spruce caused by autumn infestation. Tarenig, Wales, November 1974.

Plate 10 Defoliation of 50-year-old Sitka spruce following spring infestation by *E. abietinum.* Damage is concentrated in the lower canopy. Hafren Forest, Wales, September 1997.

Plate 11 Young Sitka spruce defoliated by *E. abietinum* and damaged by late spring frost, a potentially lethal combination. Korsoe, Denmark. *(S. Harding)*

Plate 12 Complete defoliation of road-side Sitka spruce. Selkirk, Scotland, September 1997.



Plates 13 and 14 Alate and apterous *E. abietinum* killed by entomophthorales fungus. *(S. Westergaard)*

Plate 15 *E. abietinum* killed by entomophthorales. Infected individuals often cluster on the stem. *(K. Day)*

Plate 16 Parasitized *E. abietinum:* the dry cuticle of the aphid left behind after the adult parasitoid wasp has emerged (via the flap at the rear of the aphid).

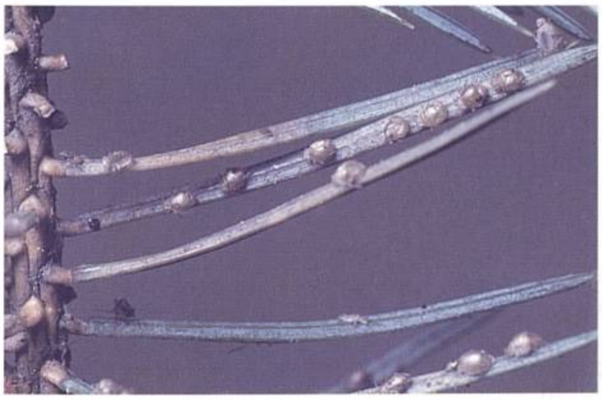


Plate 17 Numerous *E. abietinum* 'mummies' attached to the needles of Sitka spruce indicative of a high rate of parasitism.

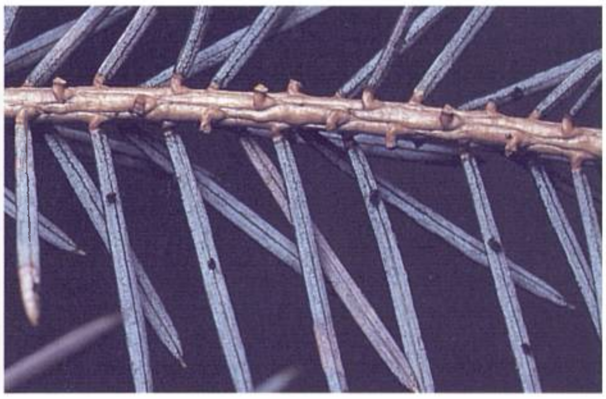


Plate 18 *E. abietinum* killed by frost. The black, shrivelled aphids remain attached to the needles.

Plates 19 and 20 Variation in the amount of defoliation caused by *E. abietinum* in a young Sitka spruce plantation. Defoliated and undefoliated trees often occur side by side.

Plate 21 Two individuals of the same Sitka provenance showing susceptibility (left) and resistance (right) to *E. abietinum* attack. Ulborg, Denmark. *(S. Harding)*

Plate 22 Hafren Forest, Wales. A typical upland commercial forest in the UK comprised largely of Sitka spruce.

Plate 23 Sitka spruce plantation at Alstahaug, Nordland, Norway. *(Bernt-H. Øyen, NISK)*

Plate 24 P49 Sitka spruce at Haukadalur, south Iceland. *(T. Benedikz)*

Chapter 2

Damage sustained by individual trees: empirical studies on the impact of the green spruce aphid

Nigel A. Straw, Gudmundur Halldórsson and Thorarinn Benedikz

Summary

Empirical studies on the impact of *E. abietinum* on Sitka spruce have been conducted in Britain, Ireland, Norway and Iceland, and have involved manipulative experiments on pot-grown plants in nurseries and young trees in the field, and observations on the effects of natural outbreaks in plantations. Differences in methodology, tree age, growing conditions and other factors hinder direct comparisons between studies, but certain general patterns in tree response can be identified. Height increments are reduced, on average, by 10-30% by the end of the season following severe or complete spring/early summer defoliation. Further reductions in height increment may occur in the following 1-3 years. Reductions in stem diameter increment are of a similar magnitude but, in contrast to height growth, occur primarily in the following year or even after a longer period. The effect on diameter increment in the year of attack is usually small. In the oldest trees studied, diameter increments were suppressed for up to 7-8 years. The different response of height and diameter growth is probably caused by a strong direct effect of aphid feeding on leader extension at the time of infestation, followed by a more typical, delayed response of both diameter and height increments to the loss of needles. Fertilizer treatments and SO_2 pollution appear capable of modifying the impact of *E. abietinum*, by increasing tree susceptibility to attack, by promoting higher aphid population densities and by altering the tree's growth response to defoliation. However, information on these and other potential modifying factors is limited, and many general patterns in the response of Sitka spruce to infestation by *E. abietnum* have yet to be established.

Introduction

The importance of green spruce aphid (*Elatobium abietinum*) as a forest pest lies in its ability to cause extensive defoliation, especially of Sitka spruce, and the impact that defoliation may have on tree growth. The aphid rarely kills trees in Europe and its main effect is to reduce annual growth increments (Bevan, 1966; Carter, 1977). This arises because the aphid infests only the one-year-old and older needles. The new needles are chemically defended for the first few months and are not colonised until the autumn (Jackson and Dixon, 1966), with the result that trees always carry some foilage after spring and early summer infestation, or soon regain foilage after autumn or winter attack. This is usually enough to ensure that trees survive and eventually recover. The death of small or large trees may occur under execptional conditions, particularly after complete autumn or winter defoliation when trees have been left bare for several months, or in combination with severe frost damage, but it is a rare phenomenon (Petersen, 1960; Bevan 1966; Halldórsson, unpublished; Harding, personal communication).

The potential of *E. abietinum* to reduce increment has been of interest for a long time, but recently a number of new studies have been completed or initiated, partly in response to the need for better quantitative information with which to advise forest managers, but also in recognition that global warming may lead to better winter survival of *E. abietinum* in the future and a greater frequency of defoliation (Straw, 1995). The forestry industry in several north-west European countries has invested heavily in Sitka spruce and any increase in the frequency and severity of attack is likely to have widespread consequences.

Information on the relationships between aphid densities, needle loss and tree growth is also important for evaluating costs and benefits of selecting spruce for resistance to *E. abietinum*, and for evaluating different management strategies, e.g. identifying gains in yield which might be obtained by reducing aphid populations through enhancement of natural enemies. Cost-benefit analyses require data on growth losses to be incorporated into either empirical yield models or forest process models (Chapter 3) which can then be used to calculate the effects of infestation on timber volume. *E. abietinum* attacks all ages of trees and can attack the same stand repeatedly during its lifetime. Mathematical models are the only means, therefore, of integrating the effects of attack over the whole forest rotation and predicting effects on final tree size. However, before model predictions can be accepted with confidence, models need to describe the response of trees to infestation and defoliation accurately, in line with the results from empirical studies.

Studies on the impact of *E. abietinum* have been conducted in Britain, Ireland, Norway and Iceland, and all have looked at effects on Sitka spruce. Comparing results from these studies is difficult, because of differences in site and climatic conditions, differences in tree age, provenance and stand history, and because of differences in the seasonal pattern of aphid infestation. *E. abietinum* populations in Britain, Ireland and Norway usually peak during spring or early summer, whereas those in Iceland peak in the autumn (Chapter 4), and early and late defoliation may have different effects on tree growth (Kulman, 1971; Larsson, 1983). Different methodologies also limit the degree of comparability between studies and influence interpretation of results. Consequently, those aspects which growth loss studies ought to attempt to quantify, under ideal circumstances, are reviewed briefly as a guide to interpreting the empirical studies which have been described.

Objectives of empirical studies

Studies on the impact of forest insect pests should, ideally, address four key questions: (1) what is the relationship between insect density and the amount of damage inflicted (e.g. percentage of needles lost, number of shoots killed), (2) by how much and for how long are annual increments depressed, and, with regard to commercial aspects, (3) what are the effects of reduced increment on final tree size and timber yield, (4) what are the economic costs of reduced yields. Financial losses arise if timber volumes at harvest are lowered or if the rotation has to be extended to allow trees to reach optimum size. Wood quality and therefore its value might also be affected.

Most growth loss studies in forest systems have looked at the effects of leaf-chewing insects and have focused on question (2), the immediate effects of defoliation on annual increments (Kulman, 1971). Such studies address the question of most immediate importance and demonstrate the capacity of insects to reduce tree growth, but most were too short to determine the total period over which increments were reduced or the time taken for the trees to resume normal growth. Without this information it is not possible to determine the total, accumulated impact of a particular outbreak (Austarå, 1984; Orlund and Austarå, 1996). Very few studies have been developed far enough to assess effects on final tree size or to calculate economic costs.

The most serious omission of growth loss studies in general, however, is the paucity of information on defoliator population levels and rates of defoliation or other damage. This information is essential if the response to insect attack of different tree species, genotypes or ages, or of trees growing on different sites, is to be compared and general patterns in growth response identified. The reasons for this lack of data are understandable. Assessing insect numbers and recording rates of defoliation is extremely time consuming and often cannot be included in experimental designs when funds are limited. In addition, the majority of field studies, particularly those on natural insect outbreaks, were initiated only after damage became noticeable and when outbreak populations were subsiding. Obtaining estimates of insect numbers and defoliation retrospectively in these situations was usually impossible.

Empirical studies on the impact of *E. abietinum* exhibit all of these problems and omissions, especially a lack of information on aphid densities and defoliation rates. This makes it extremely difficult to compare results from previous work. Early experiments and field studies were rather short and tended to measure different tree growth parameters. As a result, there is still relatively little information on the effect of *E. abietinum* on stem diameter and volume increment and on final tree size. In only one case were the economic costs of infestation estimated (Carter, 1977).

Establishing the relationships between *E. abietinum* densities, defoliation and growth loss is crucial for combining impact studies with aphid population models and hence for evaluating the impact of changes in aphid populations brought about by climate change or

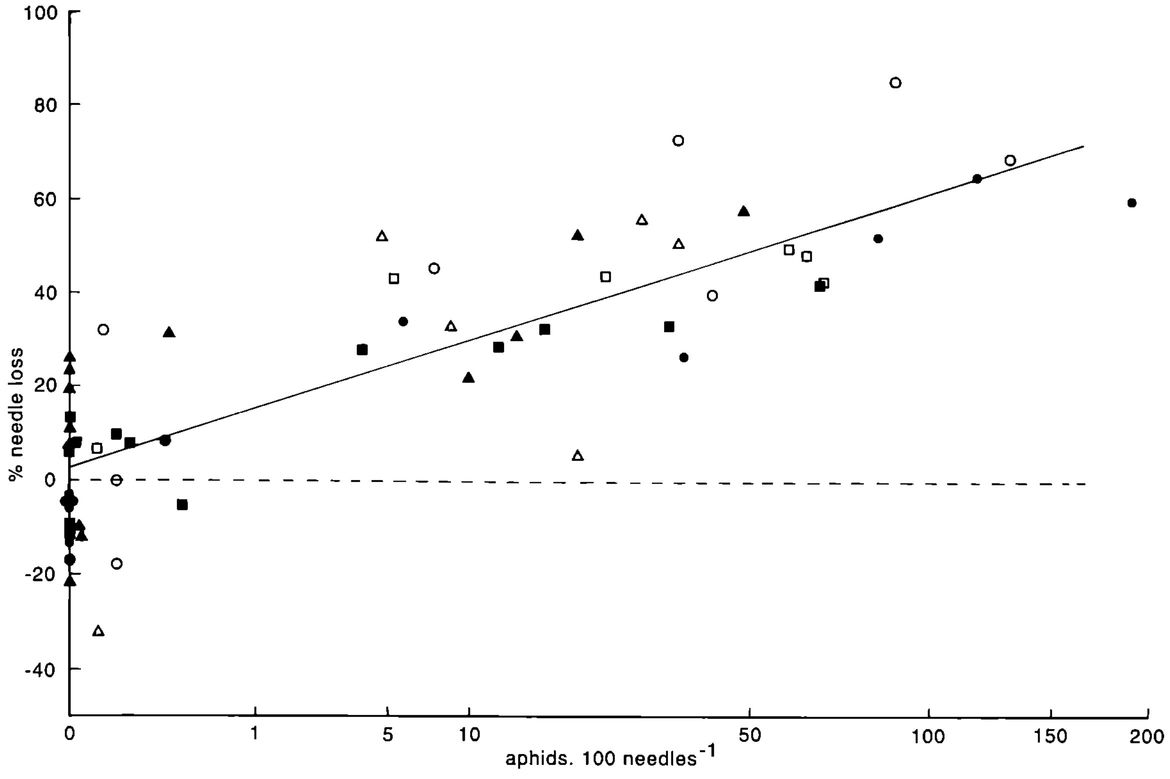


Figure 2.1 The relationship between loss of 1-year-old needles and peak *E. abietinum* density on 4-year-old Sitka spruce in Hafren Forest, Wales (from Straw *et al.*, 1998).

Percentage needle loss was calculated as the difference between needle density in May, before peak aphid infestation, and needle density in October. May needle density was adjusted to account for the natural rate of needle loss (without aphids) that would have occurred over the same period. Estimates of percentage needle loss and aphid density were obtained separately for shoots at six different positions in the canopy, and averaged for the trees in each plot. The different symbols in the Figure represent these mean values for the different canopy positions, for five plots with high aphid densities and five plots with low aphid densities (r^2=0.69, P<0.001). Variation in the estimates of needle density, arising because different shoots were assessed at each canopy position in May and October, leads to some apparent increases in relative needle density.

alternative management strategies. Recent studies have begun to examine these relationships (Figure 2.1, Straw *et al.*, 1998), although patterns need confirmation. Percentage loss of older needles on young Sitka spruce in Wales was linearly related to peak aphid densities in the spring when these were plotted on a logarithmic (or cube root) scale (Figure 2.1). This indicates an asymptotic relationship between needle loss and aphid density on an arithmetic scale in which the per capita effect declines as aphid density increases, and where complete defoliation is achieved only following very high rates of infestation. At the opposite extreme, low aphid densities appear to cause surprisingly high rates of defoliation. Densities of 1 aphid per 100 needles caused, on average, 15-20% needle loss, suggesting either greater redistribution of aphids in the canopy than previously suspected or a particularly strong physiological reaction of Sitka spruce to infestation (Straw *et al.*, 1998).

A reaction to substances introduced into the tree whilst the aphids are feeding, such as those responsible for needle chlorosis and death (Kloft and Ehrhardt, 1959; Fisher 1987), might influence growth directly. The relationship between *E. abietinum* and increment is likely to be more complex, therefore, than that between a leaf-chewing insect and increment. It could involve physiological poisoning and disruption of the hormonal control of tree growth alongside the effects of sap removal and needle loss, the latter affecting growth by reducing photosynthetic capacity and the space for storing nutrient reserves.

Studies on the impact of *E. abietinum* on increment have involved experimental work and observations on natural outbreaks. Experiments should provide the most unambiguous data. The basic approach is the same whether experiments are conducted on pot-grown plants in the nursery or on trees in the field. A randomly selected set of trees is infested with aphids and defoliated, and the performance of these trees is compared with a comparable, randomly selected set of uninfested control trees maintained under the same conditions or intermixed within the same plantation. Divergence in the performance of infested and uninfested trees gives a direct measure of the impact of infestation. Experiments on pot-grown plants have started with insect-free material and defoliated trees have been produced by inoculating plants with aphids. Field experiments have begun with the reverse situation, with most trees naturally infested and uninfested control trees obtained by spraying with insecticides. This achieves the same kind of comparison, but is dependent on obtaining high aphid populations naturally, which cannot be guaranteed, and care must be taken to ensure that insecticides are not phytotoxic or growth promoting.

Difficulties in applying treatments and problems with making detailed assessments has meant that experimental work has been restricted to trees <6 years old. It is not clear, however, whether results obtained for small trees are applicable to larger trees or can be applied at the plantation scale. Current information on the impact of *E. abietinum* on older trees in commercial plantations comes from observations on natural outbreaks. Without an experimental control, however, results from observational studies have to be treated with some caution. Estimates of growth loss have been obtained by comparing growth of the same trees before, during and after attack, or by comparing the performance of neighbouring trees that were naturally defoliated or which remained undefoliated. The dangers here are, first, that high aphid populations may be associated with weather conditions that also influence spruce growth directly with the result, for example, that growth losses in the year of attack might be partly attributable to a generally poor season for spruce growth (Koerber and Wickman, 1970) or, second, that aphids might colonise relatively slow growing or stressed trees preferentially, with the result that differences between the performance of infested and uninfested individuals might merely reflect underlying differences in inherent growth rates independent of aphid attack (see Chapter 7). *E. abietinum* populations certainly appear to benefit from certain climatic conditions that are unfavourable for spruce (Straw, 1995) and, in at least one experiment, aphid performance improved on intermittently drought-stressed trees (Major, 1990). Consequently, there are good reasons to suspect that climatic or site related factors could mask some of the affects of aphid infestation during natural outbreaks.

Impact studies in Britain and Ireland

E. abietinum causes defoliation regularly in the mild, oceanic regions of western Britain and Ireland. In these areas, *E. abietinum* maintains anholocyclic populations on spruce throughout the year. Cold periods reduce the numbers of aphids overwintering, but small numbers of individuals survive to reproduce in the spring and densities build up steadily as the weather improves. Peak populations usually occur in May or June after which numbers decline rapidly to a characteristic mid-summer low, and they remain low until the autumn (Chapter 4). Populations increase in the autumn, but they usually remain smaller than in the spring. Defoliation can occur in November and December if autumn weather conditions are particularly favourable, but damage at this time is less common. Severe defoliation is normally a result of spring infestation.

The mild and wet climate that favours *E. abietinum* is also particularly suited to Sitka spruce. Provenances from Oregon, Washington and British Columbia outperform all other conifer species grown in these climatic regions and in upland forests they typically achieve general yield classes of 14-18 (i.e. a mean maximum annual increment of 14-18 m^3 ha^{-1} $year^{-1}$) (Proe *et al.*, 1996). Most stands are thinned periodically from *c.* 20 years after establishment and are clear-felled after 40-60 years. The high productivity of Sitka spruce means that it is the most widely planted commercial tree species in north and west Britain and in Ireland. Over 530 000 ha have been planted in Britain alone since the 1920s (Forestry Commission, unpublished). *E. abietinum* occurs over the whole of this area and, consequently, its potential impact on timber production is enormous. Recognition of this potential has prompted several experimental and field-based studies to quantify the aphid's impact.

Experiments on small pot-grown trees

Three studies have looked at the effect of spring infestation by *E. abietinum* on small pot-grown Sitka spruce (Table 2.1), although the study by Warrington and Whittaker (1990) was concerned more with interactions between SO_2 pollution, drought and aphids, and spruce growth, and was not designed specifically as a growth loss study.

Carter (1977) added 100 aphids to each of 20 Sitka spruce transplants and compared their growth at the end of the season with 20 uninfested trees. Leader growth was reduced by 10% and the total length of new shoots produced was reduced slightly more, but the total dry weight (DW) of new shoots produced was reduced by about half (Table 2.1). Root DW was less affected, suggesting that aphid infestation would have altered the root:shoot ratio in favour of roots.

Warrington and Whittaker (1990) added four aphids per tree in late April, which resulted in over 300 aphids and 34.5% needle loss per tree by the end of June. The affect on leader growth was similar to Carter (1977), but less dramatic reductions were observed in shoot and whole plant DW. This may be because their study lasted only two months and the plants were harvested at the end of June before DW accumulation was complete. The early harvest date may also have affected the response in root DW. Root growth occurs later in the season than shoot growth (Kozlowski *et al.*, 1991) and root DW might have recovered substantially had the plants been allowed to grow through to the end of the season. Warrington and Whittaker (1990) also used relatively small sample sizes per treatment (nine trees) and the growth reductions attributable to *E. abietinum* that were given (Table 2.1) were averages for all treatments combined, including drought stressed trees and trees grown in elevated SO_2 conditions. The results might not be representative, therefore, of growth losses encountered under normal, well watered and unpolluted conditions.

More recently, Straw and Green (unpublished) conducted an experiment which included early, mid and late season infestation of pot-grown Sitka spruce. Fifty plants were inoculated with either three 3 cm pieces of infested shoot material during mid or late April, or in early May 1994, or were left without aphids as controls. Height, leader length, stem diameter and needle densities were recorded at the end of 1994 and 1995, and sub-samples of 10 plants per treatment were harvested for DW components at the same time. Preliminary results from this experiment show that in 1994, the year of infestation, leader growth was reduced by about the same amount as in the earlier studies, but less affect was observed on total shoot length and shoot, root and total plant DWs. Root and shoot DW were affected to about the same extent, suggesting no immediate impact on root:shoot ratios. Early infestation had a greater impact than mid and late spring inoculations. The experiment confirms, therefore, Carter's (1977) results for tree height increment in the first year, but does not support the much relatively greater effect on shoot DW. In the second year after infestation, affects on leader growth were again pronounced and similar to those in the first season (Table 2.1). Total shoot length produced and new shoot, total root and total plant DWs were also reduced further and by more than in the first year.

Table 2.1 Experimental studies on two-year-old, pot-grown Sitka spruce. Growth loss determined by comparing aphid-infested trees with uninfested controls

	Leader length	Total length of shoots produced	DW shoots produced	DW roots	DW whole plant
(a) Percentage reduction in growth at the end of the season in which infestation occurred.					
Carter (1977)	10%	18%	48%	7%	55%
Warrington and Whittaker (1990)[1]	13%	-	15%	21%	19%
Straw and Green (unpublished)					
- early infestation	25%	17%	15%	15%	15%
- mid infestation	14%	7%	6%	6%	8%
- late infestation	2%	6%	5%	5%	6%
(b) Percentage reduction in growth at the end of the second year					
Straw and Green (unpublished)					
- early infestation	24%	29%	27%	21%	22%
- mid infestation	15%	14%	10%	11%	12%
- late infestation	9%	7%	5%	13%	11%

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[1] 34% defoliation by the end of June.

Table 2.2 Observations on natural *E. abietinum* outbreaks in plantations

	Tree age[1]	Defoliation	year 1	year 2	year 3
(a) impact on height increment (leader length)					
Carter (1977)	5-6	complete	40-54%*	45-61%	-
(N.E. England)		(1971)			
Carter and Nichols (1988)	6	complete	42-61%*	22-44%	-
(S. Wales)		(1980)			
Thomas and Miller (1994)	11-12	minor	12%*	16%*	18%
(E. Scotland)		major	19%*	34%*	14%
		severe	31%*	50%*	48%
		(1988-89)			
Seaby and Mowat (1993)	15	severe[2]	25%*	-	-
(N. Ireland)		complete	31%*	-	-
		(1980)			
(b) impact on diameter increment (at 1.3m)					
Thomas and Miller (1994)	11-12	minor	9%*	15%*	6%
(E. Scotland)		major	12%*	40%*	19%
		severe	33%*	56%*	33%

* year of defoliation (subsequent years aphid-free)

[1] age (years) when defoliated

[2] 53.5% loss of older needles

Studies on natural outbreaks

Comparisons of the growth performance of naturally defoliated and undefoliated trees have been made by several researchers in Britain and Ireland (Table 2.2). In all of these studies defoliation appears to have been the result of severe spring infestation. Growth was recorded as height or diameter increments, the latter at 1.3m (diameter at breast height, dbh). The studies fall into two groups: those of Carter (1977) and Carter and Nichols (1988) on 5-6 year old trees in a commercial plantation and a IUFRO provenance trial, respectively, and those of Seaby and Mowat (1993) and Thomas and Miller (1994) on older trees being monitored as part of fertilizer experiments. Carter (1977) compared the height growth of two cohorts of naturally infested and uninfested trees before and after an *E. abietinum* outbreak in 1971, whereas Carter and Nichols (1988) compared the height increments of five different Sitka spruce provenances for the two years before, and two years after, a similar defoliation episode in 1980. The range of growth loss estimates given for these studies (Table 2.2) represent the response of the different cohorts or provenances. In both studies, reductions in height increment amounted to about 50% in the year of attack and a similar amount in the following aphid-free year.

In contrast, Seaby and Mowat (1993) and Thomas and Miller (1994) recorded smaller reductions, at least in the first year. These results might suggest that older trees are less affected by *E. abietinum* than younger trees, but this is probably not the case since the circumstances of each study were rather different. The trees monitored by Carter (1977) and Carter and Nichols (1988) appear to have been defoliated much earlier in the spring than those studied by Seaby and Mowat (1993) and Thomas and Miller (1994) and this may have resulted in a greater impact on growth. Average defoliation rates may have differed, although needle loss was recorded as either severe or complete in all of the studies. However, detailed assessments of needle loss and the timing of attack were not made.

The studies of Carter (1977) and Carter and Nichols (1988) were initiated after single, intense episodes of infestation and the following years were aphid free. In contrast, the trees analyzed by Thomas and Miller (1994) were defoliated over two years (1988 and 1989), and the larger impact on growth recorded in the second season was probably a response to an accumulated amount of damage. The trees on this site must have been damaged in spring of 1988, since height increments were reduced significantly in that year, and visual assessments and litter trap catches indicated further substantial infestation in April and May 1989. The results from this study, are not, therefore, directly comparable with those of Carter (1977) and Carter and Nichols (1988) and represent the impact of a more protracted period of defoliation. There is also some difficulty in interpreting the estimates of growth loss, because the height increments of those trees recorded as most severely defoliated in April 1989 were also smaller in 1987, evidently before the aphid outbreak developed, implying perhaps that the aphids attacked slower growing trees preferentially.

Thomas and Miller (1994) compared the average height increments of plots of trees which differed in their mean scores for defoliation. They also measured effects on mean diameter increment (dbh) per plot in the same manner and found a similar pattern of response. Diameter increment was reduced in the first year of defoliation, showed greater reductions (up to 56%) in the second year, and was also reduced in the third year (Table 2.2). The fertilizer treatments in the experiment were applied in April 1989 during the second period of aphid infestation. Height growth did not show a response to the nutrient addition by the end of the study, but stem diameters were improved, particularly in response to P addition, and there was some evidence that growth losses were less severe and the trees recovered faster where fertilizer had been applied.

The fertilizer treatments in the experiment studied by Seaby and Mowat (1993) were applied much earlier, several years before the *E. abietinum* outbreak which defoliated the trees, and tree growth, the intensity of attack and impact of defoliation, were all related to N and P application (see below). The effect of defoliation on growth was calculated by regressing height increments (as a percentage of the pre-outbreak increment) against measurements of needle loss on individual trees, for different fertiliser treatments or dominance class. Needle loss, caused by infestation sometime during the previous winter or spring, was assessed in June. Subdominant trees showed significantly more needle loss (65%) than dominant trees (55%), but their response to defoliation was similar.

The growth reductions measured by Seaby and Mowat (1993) for the first season after defoliation were, overall, very similar to those observed by Thomas and Miller (1994), but the conditions on the site and the subsequent pattern of tree growth were very different. The fertilizer experiment had been laid out on an oligotrophic blanket bog at a close spacing (1.5 x 1.5 m), and the trees were evidently severely nutrient limited. All trees, whether defoliated or not, showed declining rates of growth over the period of measurement, probably because of increasing competition for light and increasing shortage of nutrients. The relative differences in growth recorded in the first year between defoliated and undefoliated trees were repeated in the next four years and there was no evidence of any recovery. The most severely defoliated trees tended to be more likely to go into growth check. Only the apparent impact on growth in the first year is given in Table 2.2, since it is not clear to what extent reductions in growth in subsequent years were influenced by the steadily deteriorating conditions. The estimates of impact obtained by this study may not be representative, therefore, of the response of trees on better sites.

Field experiments

Field experiments on the impact of *E. abietinum* are a relatively new development and have been established to obtain more precise information on the relationships between aphid density, defoliation and various measures of tree growth. Carter (1995) carried out an insecticide exclusion trial on 15-year-old Sitka spruce in Afan Forest, south Wales, but aphid densities over the five year period of observation remained low and no significant effects on tree growth could be identified. Subsequently, Straw *et al.* (1998) have manipulated *E. abietinum* densities in a four-year-old Sitka spruce plantation in Hafren Forest, mid Wales, using insecticide exclusion and inoculation of trees with aphids. Natural aphid densities also remained low in this experiment, but the inoculation treatment resulted in moderate-severe defoliation and a significant effect on growth.

The three basic treatments in this latter experiment (natural infestation, insecticide exclusion, artificially raised densities) were each applied to five replicate plots of 25 trees (Straw *et al.*, 1998). Differences in tree performance between treatments were used to determine impact on height growth, stem diameter and volume, side shoot growth and needle size. Plots and treatments were established in 1992 and inoculations with *E. abietinum* in the high density treatment were made in April 1994. Aphids were eliminated from trees in the exclusion treatment by spraying with pirimicarb (Pirimor®, ICI), a widely used aphicide which is non-phytotoxic to Sitka spruce and has no apparent growth promoting properties (Straw *et al.*, 1996). Aphid densities, needle loss and tree growth have been measured annually up to 1996. Aphid densities on the inoculated trees reached, on average, 19-20 aphids per 100 needles by June 1994 and caused 38.5% defoliation of the older needles (Straw *et al.*, 1998). Few aphids were present in 1995 and

Table 2.3 Impact of *E. abietinum* on 4-5-year-old Sitka spruce in Hafren Forest, Wales[1]. Results from a manipulative field experiment (Straw *et al.*, unpublished)

	Percentage reduction in:	
	1994*	1995
(a) incremental growth		
height (leader length)	22.4%	11.5%
stem diameter[2]	-	9.6%
stem volume	-	18.5%
(b) total tree size		
height	11.7%	10.8%
stem diameter[2]	-	6.0%
stem volume	-	11.4%

* year of defoliation (subsequent years aphid-free)

[1] effect of an overall defoliation of 38.5% of the 1991-1993 needles per tree.

[2] average reduction. Reductions in diameter increment varied 7-13% and in total diameter 3-9% for different internodes along the stem.

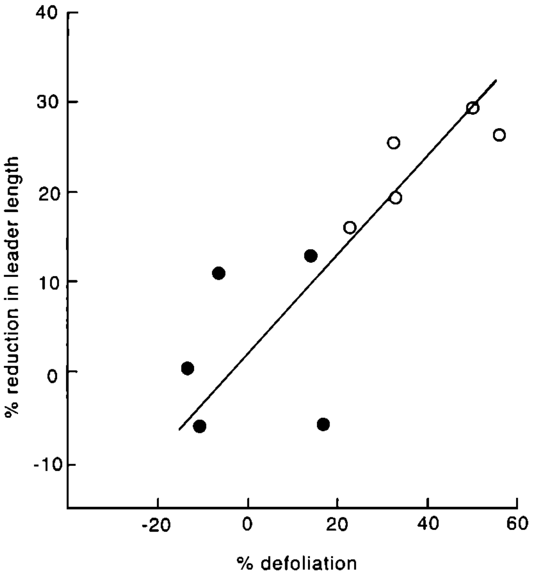

Figure 2.2 Relative reduction in height increment in the year of infestation in relation to defoliation of older needles by *E. abietinum*: response of 4-year-old Sitka spruce in Hafren Forest, Wales. Data points are plot means for the high aphid density (+++E) treatment (○) and the sprayed (-E) treatment (●).

1996. The experiment also includes treatments to assess the impact of spruce root aphids (*Pachypappa* and *Pachypappella* spp., Pemphigidae) on the site, but populations of these insects have been low and have had no significant effect on the trees.

A comparison of the growth of trees inoculated with *E. abietinum* with those in the other treatments gives an estimate of the impact of a typical, moderate-to-severe period of spring infestation (Table 2.3). Leader growth in 1994 was reduced significantly, by an amount similar to that recorded in experiments on pot-grown plants and after some natural outbreaks, and was also reduced in the following year, although by a lesser amount. The degree of growth loss was related to the amount of defoliation (Figure 2.2). Stem diameter and volume increments were not affected in 1994, the year of infestation, but were reduced in 1995 (Table 2.3).

Although the overall amount of defoliation per tree in this experiment appears rather low, aphids and needle loss were not equally distributed through the canopy and were concentrated toward the top. The 1993 leader shoot and upper whorl branches of trees in the high aphid density treatment lost 60-70% of their older needles, on average, whereas side shoots on the lower branches lost less than 5%. Reductions in subsequent shoot growth followed this pattern with the leaders being most affected and the bottom side shoots the least. The size of needles produced in 1994 was also reduced, but mainly on the upper, more heavily infested branches (Straw *et al.*, 1998).

Impact studies in Norway

Sitka spruce is an important timber species in Norway even though the main commercial conifers are Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*). Over 44 000 ha of Sitka spruce have been planted in west and north Norway since the early 1920s. In these regions Sitka spruce forms 2-4% of the total commercial forest area (spruce, pine and hardwoods) and 10-20% of the area planted with spruce (Austarå, personal communication). Thinning regimes, rotation lengths and productivity are similar to upland Sitka spruce plantations in Britain (Bauger, 1961). *E. abietinum* populations in Norway are primarily anholocyclic, although overwintering eggs are found sporadically as in Britain (Carter and Austarå, 1994), and the main population peak occurs in late spring or early summer.

The first serious outbreak of *E. abietinum* on Sitka spruce in Norway occurred in 1957 and further mass-outbreaks have occurred subsequently, affecting plantations from southern-most counties to the far north (Orlund and Austarå, 1996). Heavy infestations occurred in coastal districts of Møre and Romsdal county during the period 1987-1990 and, following this infestation, Orlund and Austarå (1996) took the opportunity

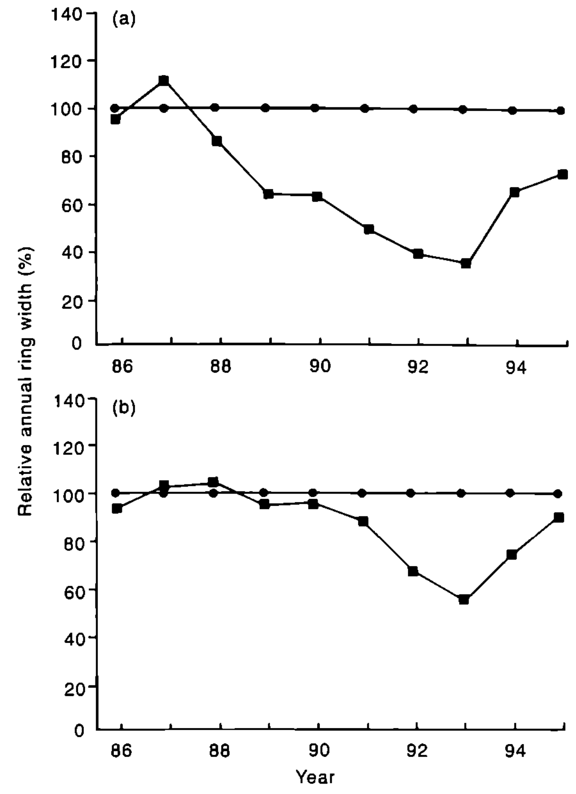

Figure 2.3 Effects of defoliation by *E. abietinum* on the diameter growth of pole-sized Sitka spruce in west Norway (from Orlund and Austarå, 1996). (a) trees with dbh ≥ 20cm; (b) trees with dbh > 15cm; ● mean annual ring widths of uninfested, control trees, standardised to 100%; ■ corresponding ring widths for infested trees, as a percentage of the controls.

to compare the diameter growth of defoliated and undefoliated trees. Core samples were taken from trees in two defoliated plots and one undefoliated plot near Molde, in Fraena municipality, in 1993 and two of these plots were re-sampled in 1995. Trees in the re-sampled plots were 42 years old at the second sampling date. Both of these plots were located in the same stand, with one plot in part of the stand which was naturally infested and the other 30 m away in a part of the stand which had remained uninfested. 190 and 271 trees were sampled in each plot, respectively, and these were divided into three size classes (dbh > 15cm, dbh 12-15 cm, dbh <12cm). Mean annual growth rings for the defoliated and undefoliated trees in each class were analysed separately. Trees with dbh ≥20 cm were also analysed as a separate group. Ocular assessments of canopy condition in 1993 indicated that defoliation was comparable to the moderate to severe rating of Thomas and Miller (1994).

The defoliated trees, particularly those in the larger diameter classes, showed a protracted period of reduced growth starting during the period of infestation and continuing for some time afterwards (Figure 2.3). Minimum ring widths occurred six years after first infestation, being preceded by several years of declining growth and followed by 2-3 years of recovery. For trees >15cm dbh, annual ring widths were suppressed on average by 18.5% for 7 years compared with the controls, a loss in growth increment of 1.3 years of normal growth (Figure 2.3(b)). Effects on the largest trees were stronger. Average ring widths in trees ≥20cm dbh were reduced by 40.5% for 8 years, equivalent to 3.2 years of normal growth (Figure 2.3(a)).

Growth loss was less pronounced for the smaller diameter size classes and the smallest trees even showed a relative increase in growth during the first 4 years of infestation. This was probably related to heavier and earlier defoliation of the taller, dominant trees which allowed more light to reach canopies lower in the stand. Diameter growth of the smaller trees declined later, presumably as the taller trees regained their full complement of foliage. However, the maximum reduction in annual increments observed in the two smaller diameter classes was only 20% compared to 55% for trees >15cm dbh and 64% for trees ≥20cm dbh. The improved light environment following defoliation appeared, at least initially, to benefit the smaller trees and may perhaps have more than compensated for a modest amount of defoliation.

Impact studies in Iceland

Sitka spruce is an important component of reforestation programmes in Iceland, but it has suffered a series of major *E. abietinum* outbreaks since the aphid was introduced into the country in 1959 (Chapter 1). At the time of settlement in the late 9th century birch scrub and forest is thought to have covered some 25-30% of Iceland (Thorsteinsson, 1972). These woodlands were more or less destroyed soon after settlement and today forested land covers only 1% of the country. Deforestation led to tremendous soil erosion and today 60% of the country is barren (Blöndal, 1994). Reforestation began at the beginning of this century and many tree species were introduced in trials (Bjarnason, 1957). Suitable provenances of Sitka spruce were not introduced, however, until the 1930s, although attempts were made to cultivate seedlings during the earliest years (Flensborg, 1905). Since then many provenances from Alaska have been planted and Sitka spruce has become one of the most important tree species (Freysteinsson, 1995). Mean annual volume increment of young Sitka stands varies between 4 and 10 m^3 ha^{-1} yr^{-1} (Blöndal, 1996). Since 1945 Sitka spruce and other North American spruces, e.g. *Picea engelmannii* Engelm., *P. glauca* (Moench) Voss and *P.* x *lutzii* Little, have represented 10% of total plantings, amounting to some 4-5 million trees annually over the past decade. By far the largest areas suitable for production forestry are in South Iceland and in 1997 parliament approved a resolution to substantially increase funds for afforesting inland sites in the southern region. Sitka spruce will be the main species planted.

Green spruce aphid is the only significant insect pest on Sitka spruce in Iceland. Major outbreaks have occurred in 1964, 1977, 1984, 1987, 1991 and 1996 (Ottósson, 1985; Blöndal, 1988; Chapter 1). Sitka spruce and other North American spruces were heavily defoliated during these outbreaks, all of which involved severe infestation during the autumn/early winter. Studies designed to estimate the influence of aphid attacks on the growth of Sitka spruce in Iceland were initiated, therefore, in view of the key role which Sitka spruce and other spruces will play in future reforestation.

Field studies

Four locations for measuring the influence of *E. abietinum* on tree growth were selected during 1992 following the aphid outbreak of 1991. Two of the study sites were located in East Iceland (Hallormsstadur and Jórvík), one in South Iceland (Tumastadir) and one in West Iceland (Sauraskógur). The main study area has been Hallormsstadur, however, since this is the only site which is homogenous both in terms of site conditions and plant material.

The site at Hallormsstadur is about 2 ha in area and was planted with Cordova (Alaskan) provenance Sitka spruce in 1960. The first major outbreak of *E. abietinum* on this site occurred in 1986-87. A second, more severe outbreak started in 1990 and culminated in 1991. Initial sampling and estimates of defoliation rate at Hallormsstadur and the other three sites was carried out in 1992. Sample trees representative of three different classes of defoliation were selected: Class I, slight or no defoliation (0-10% needle-loss); Class II, moderate defoliation (15-40% needle-loss); Class III, severe defoliation (50%+ needle-loss). These classes were not selected to represent the average degree of defoliation at each location, but were used to provide comparative material between which growth losses could be determined. Needle-loss for each sample tree was estimated visually and dbh and total height were also measured. Core samples were taken at breast height from each tree during the winter of 1992-93 and 1993-94, and further samples were taken during the winter of 1995-96. Annual rings widths in the cores were measured (to the nearest 0.1 mm) at the Norwegian Institute for Forest Research (NISK) in Bergen. Leader length of all the sampled trees has been measured annually since 1992. The length of previous leaders back to 1983-84 were measured retrospectively during the winter of 1993-94.

Effects on height and diameter growth

Height and diameter increments of the trees in the three damage classes at Hallormsstadur were similar up to 1987. Since then a clear differentiation can be seen to have occurred following the outbreaks in 1986-87 and 1990-91, both in diameter and height increment (Figures 2.4 and 2.5). The diameter increment of the defoliated trees was reduced by *c.* 10-20% compared with the slightly/undefoliated trees in 1988. The increment of the severely defoliated trees was further reduced in 1989, whereas trees with lighter damage made a slight recovery. The situation remained more or less stable in 1990 and 1991, but a large reduction in diameter increment in defoliated trees occurred in 1992, when the increment of the severely defoliated trees was reduced by over 50% and that of the moderately damaged trees was reduced by about

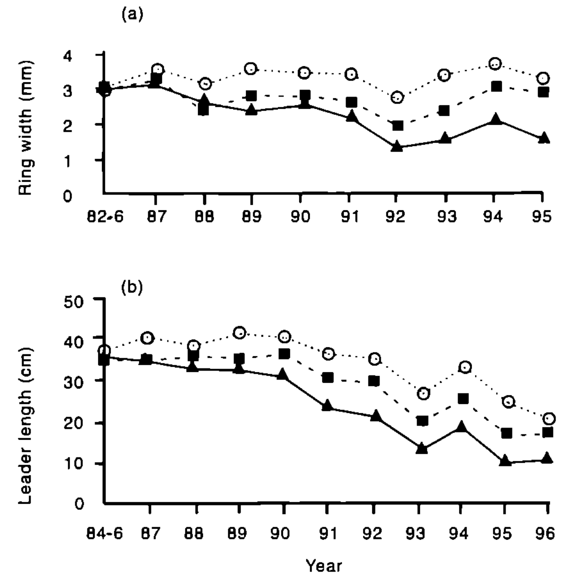

Figure 2.4 Annual diameter increments (a) and annual height increments (b) of 36 year-old Sitka spruce at Hallormsstadur, Iceland, for the period 1982-1996. ···○·· slightly /undefoliated trees (Class I: 0-10% needle loss); —■— moderately defoliated trees (Class II: 15-40% needle loss); —▲— severely defoliated trees (Class III: >50% needle loss).

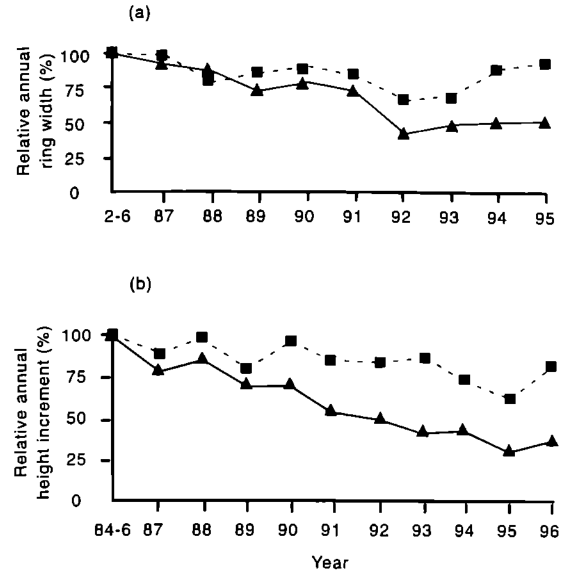

Figure 2.5 Annual diameter increments (a) and height increments (b) of moderately (Class II) and severely (Class III) defoliated Sitka spruce relative to the increments of the slightly/undefoliated trees at Hallormsstadur, Iceland, for the period 1982-1996. -■- Class II trees (15-40% needle loss); -▲- Class III trees (>50% needle loss).

33% compared with the slightly/undefoliated trees. By 1995 the moderately defoliated trees had almost recovered, whilst the severely damaged trees had only made a slight recovery (Figure 2.5a).

A somewhat different pattern was observed for height growth. A relative reduction in height increment of defoliated trees was observed in 1987 and this trend continued until 1989 as far as the most affected trees were concerned, when height increment of these trees was reduced by 25% compared with that of the slightly/undefoliated trees. The situation was less clear for trees with 15-40% needle loss. Both defoliated classes of trees suffered a further loss in increment in 1991 and this development continued until 1995, when height increment of the most affected trees was only about a third of that of the slightly/undefoliated trees. Recovery of defoliated trees started in 1996 (Figure 2.5b).

These results show that *E. abietinum* has a very considerable effect on the growth of Sitka spruce in Iceland and that the trees are slow to recover. The response of diameter increment to aphid attack seems to be different to the response of height increment. Reduction in height increment occurred immediately after attack, whereas there was a lag of one year before diameter increment was affected. Thus height increments were reduced in 1987 following initial infestation in autumn 1986, whereas diameter increments were reduced for the first time in 1988. A similar pattern was observed after the 1990-91 outbreak. Diameter increments recovered earlier. Growth of trees at the other sites showed a similar pattern (Halldórsson and Benedikz, unpublished), although the recovery of trees at the other sites was faster than at Hallormsstadur. The reason may be that the inner Fljótsdals area, to which Hallormsstadur belongs, is climatically too dry for Sitka spruce to realise its full growth potential, except on sites which receive ample soil moisture. The annual height increment on this site seems to be slowing down unusually early, possibly indicating that the trees have reached the size at which moisture may be limiting growth.

Influence of environmental and climatic factors on impact

Environmental and climatic factors can modify the impact of *E. abietinum* on spruce through three different routes: (1) they can promote greater aphid population densities which will cause more damage; (2) they may change the relationship between aphid densities and needle loss, and (3) they may modify the growth response of the trees to a given rate of infestation or needle loss. Temperature and related climatic factors, within their normal range of variability, influence impact through their effect on aphid population development (Chapter 4) and form an integral part of any study on the interaction between *E. abietinum* and spruce. Extreme climatic conditions, however, and certain anthropogenic factors can modify impact over and above that which would otherwise normally occur. Such factors include nutrient supply, as influenced by fertilization, atmospheric pollution and drought.

Fertilization

The fertilizer experiments of Seaby and Mowat (1993) and Thomas and Miller (1994) provided an opportunity to compare the impact of *E. abietinum* on trees growing under different inputs of nitrogen (N) and phosphate (P). The experiment studied by Seaby and Mowat (1993) was laid out on a nutrient deficient blanket bog and the initial fertilizer treatments had been applied by ground application in 1975, five years before the *E. abietinum* outbreak. Tree growth responded strongly to N and P addition (Table 2.4), but nutrients appear to have become increasingly limiting as time progressed and by the end of the study some trees were showing signs of growth check.

Table 2.4 Interaction between the impact of *E. abietinum* and fertilizer treatment (after Seaby and Mowat, 1993)

Fertilizer treatment[1]	% reduction in leader length at 100% defoliation[2]	leader length at zero defoliation as a percentage of the mean 1977-79 leader length[3]
N 0	28%	87%
N 1	30%	86%
N 2	30%	94%
N 3	42%	105%
P 1	28%	88%
P 2	32%	95%
P 1, N 0	10%	75%
P 2, N 3	45%	110%

[1] N 0-3, four nitrogen levels irrespective of phosphate level; P 1, 2, two phosphate levels irrespective of N level; P 1 N 0 and P 2 N 3, comparison of the lowest and highest levels of fertilizer application.

[2] calculated as the slope of the regression of mean 1980-81 leader length as a percentage of 1977-79 (pre-defoliation) leader length against defoliation of 1977-79 needles.

[3] calculated as the intercept constant of the regression of 1980-81 leader length (as above) against defoliation.

Following defoliation by *E. abietinum* in 1979-80, the intensity of attack was related to the level of nutrition. Trees in the high N plots tended to be more heavily defoliated than trees in the low N plots. The degree of growth reduction showed the same trend and was significantly different between treatments (Table 2.4). Impact on growth was greater in the high N and high P plots. There was an inverse correlation between impact on height increment and potential leader length that could have been achieved, as related to nutrient supply (Table 2.4). This was probably because the capacity of the most nutrient limited trees to respond to defoliation was restricted because of their generally poor performance.

Thomas and Miller (1994) looked at a more typical Sitka spruce plantation and compared simulated wet deposition of N and NPKMg with ground applications. However, their treatments were first applied only at the time of the *E. abietinum* infestation and they did not find any significant difference between the intensity of attack and fertilizer addition. Potential height increment and the response to defoliation were not related to fertilizer treatment, but diameter increments were affected. N addition caused a 12% increase in diameter increment and P addition a 23% increase, and it appeared that the reduction in diameter growth was less, and recovery following defoliation was more rapid, on trees in the high nutrient regimes. There was some evidence, therefore, that fertilization might ameliorate some of the effects of severe *E. abietinum* outbreaks and speed the recovery of the trees by replacing some of the N and other nutrients lost during needle fall.

Atmospheric pollution

McNeill and Whittaker (1990) found that short-term exposure of potted Sitka spruce seedlings pre-fumigated with 100 ppb (nl litre^{-1}) SO_2 increased the mean relative growth rate of *E. abietinum*, suggesting that SO_2 pollution might lead to higher *E. abietinum* populations (Chapter 8). This was confirmed by the fumigation experiment conducted by Warrington and Whittaker (1990) which looked at the interaction of SO_2, drought and *E. abietinum* on the growth of pot-grown Sitka spruce. Aphid numbers on watered, two year old trees that were maintained in 25 nl litre^{-1} SO_2 between 28 April and 28 June reached 985 ± 223 (s.e.) per tree by the end of the experiment (following addition of four aphids per tree on 28 April), whereas aphid numbers on watered trees grown in ambient air reached only 309 ± 90 aphids per tree.

Sulphur dioxide had no direct affect on plant growth (i.e. growth loss was little affected by pollution alone), but growth loss caused by *E. abietinum* was broadly proportional to the number of aphids. Consequently, because SO_2 promoted higher aphid numbers more damage was caused to the SO_2 fumigated trees. A significant interaction in the effect of aphid and SO_2 was seen only in leader extension growth and root DW. Both were reduced by more, 22% and 26% respectively, than would have been expected from the additive effects on these growth parameters of aphids and SO_2 acting alone.

Drought

Warrington and Whittaker (1990) found that, unlike SO_2, drought had a large, direct effect on Sitka spruce, similar to that caused by aphids alone, but that the combined affects of drought and aphids were less than additive. Drought had little effect on aphid numbers. Aphids on plants in ambient air which were not watered after 25 May reached 422 ± 61 aphids per tree, a 1.5-fold (but not significant) increase over aphids on plants kept in ambient air and watered throughout the experiment. Drought and aphids interacted significantly for three parameters: current season above ground growth, root DW and total plant DW. In all cases, the interaction indicated a less severe effect than that expected. The reason for less than additive affects may have been that the effects of drought and aphids alone were so severe that there was insufficient capacity left in the trees to show any further substantial growth loss.

Interaction between factors

Drought made trees fumigated with SO_2 less acceptable to *E. abietinum*. Aphid populations reached 626 ± 140 aphids per tree in the drought x SO_2 fumigation treatment, compared with the >900 aphids per tree in the watered x SO_2 fumigation treatment. However, this was still twice the number of aphids on the control trees (i.e. well-watered trees in ambient air). Consequently, growth loss was less than for watered trees fumigated with SO_2, which carried higher aphid populations, but was more than for watered and drought-stressed trees grown in ambient air. Overall, the capacity of low SO_2 concentrations to increase aphid populations had a greater effect on tree growth than that caused by drought, even though the latter was severe and reduced growth directly.

The only significant interaction between SO_2, drought and aphids on growth was in root DW where the combined effect was less than additive (22% less than expected from the independent effects), although this result may have been affected by the early harvest date. It is also possible that, as above, there was insufficient plasticity left in the growth response of the trees when all of the different environmental factors were combined.

Discussion

Studies on the impact of *E. abietinum* provide examples of all of the various methods which can be used to quantify the effects of insects on tree growth: experiments on young trees in pots or in the field, and observational and tree ring studies on older trees in plantations. Each methodology has particular limitations and produces different kinds of results, and any general patterns in tree response identified must take these limitations into account. However, several key features of the response of Sitka spruce to *E. abietinum* have emerged, particularly in relation to effects on height growth and differences in the response of height and stem diameter.

Effect on height growth

Infestation by *E. abietinum* in spring or early summer, before or at the time of shoot extension growth, has an immediate effect on height increment. In Britain and Ireland, the length of the leader shoot produced in the year of attack was always reduced. In Iceland, where populations of *E. abietinum* peak in the autumn after the trees have become dormant, height increments were affected in the following year. At Hallormsstadur, height increments were reduced for 3-5 years after each two-year outbreak. Other studies have only monitored height growth for two years, but the reductions in growth in the second year suggest that in these cases also height increments would not have returned to normal in the third or perhaps even the fourth year after infestation.

The amount by which height increments are reduced is fairly consistent. The experiments and the field observations of Seaby and Mowat (1993) and Thomas and Miller (1994) all indicate a reduction in height increment of 10-30% after severe or complete spring/early summer defoliation. Carter (1977) and Carter and Nichols (1988) obtained higher estimates, but this may have been the result of the trees being defoliated very early in the spring, well before budburst. Carter (1977) described an experiment in which 2-year-old Sitka spruce were defoliated by hand in December or in May. December defoliation reduced leader growth by 37% in the following summer and the total length of shoots produced by 54%, whereas May defoliation reduced leader length by 17% and total shoot length by 27%. Even though artificial defoliation is probably not a good simulation of the effects of *E. abietinum*, these results show that needle loss in the autumn has a greater effect on growth than needle loss in the spring. This might be expected since trees would be left without needles for a much longer period before new foliage developed after autumn defoliation, during which time reserves would be depleted to a greater extent. Autumn defoliation would also impair winter photosynthesis which is important for building up nutrient reserves prior to the start of the growing season (Bradbury and Malcolm, 1978). Even after bud-burst, earlier infestation has a greater effect on growth than later infestation (Straw and Green, unpublished; Table 2.1). Consequently, earlier infestation may explain the greater impact observed by Carter (1977) and Carter and Nichols (1988), although it is possible that differences in site and climatic conditions also played a part.

Because autumn defoliation seems to have a relatively greater affect on tree growth, *E. abietinum* might be expected to have a greater impact on Sitka spruce in Iceland than in the other European countries. However, reductions in height (and diameter) increments at Hallormsstadur were similar to those observed in Britain and Ireland. The studies are too different to allow any closer comparison.

Differences in the response of height and diameter growth

Several studies recorded effects on height and diameter increments concurrently, allowing a direct comparison to be made of the response of these growth parameters. The experimental results from Hafren Forest and observations from Hallormsstadur indicate that stem diameter increments are not reduced immediately, in the same year as spring infestation or in the growing season after autumn attack, but are affected one year later (Table 2.3, Figure 2.5). Straw and Green (unpublished) also found that the main affect on diameter increment occurred in the second season after spring infestation. In their early infestation treatment, stem diameter increment was reduced, on average, by 8% in the year of infestation, and by 14% in the following year.

In contrast, Thomas and Miller (1994) found that effects on diameter increment were similar to those on height increment (Table 2.2). Both parameters were reduced in the year in which defoliation was first recorded and by about the same amount. However, the height increments of trees recorded as most severely defoliated in this study were also relatively smaller in the previous year, before defoliation was assessed. This could mean that aphids colonised slower growing trees on this site preferentially (although see Chapter 7), but it could also indicate that there was significant infestation in the spring of the previous year and that height increments were affected initially a year earlier. If this were the case, then the observed effect on diameter could be the main effect occurring after a lag of one year, compatible with the delayed effect seen in other studies.

A delay of one year in the main response of stem diameters to defoliation is the more typical reaction (Straw, 1996). Reductions in growth in the year of attack are usually limited because growth is largely predetermined at the time of bud set at the end of the previous season (Kulman, 1971; Kozlowski *et al.*, 1991). In the year in which damage occurs, reduced photosynthetic capacity and the smaller quantity of reserves accumulated impairs the formation of bud and cambial primordia and leads to a decrease in growth in the following season. A delayed response in stem diameter (and stem volume) increment in Sitka spruce is not, therefore, unexpected. Day and McClean (1991) analysed the effects of endemic populations of *E. abietinum* on the growth of 10-18 year old Sitka spruce in N. Ireland and found that diameter increments (as basal area) were most closely correlated with aphid densities recorded two years previously.

Height growth may also show a delayed response to defoliation (Kulman, 1971; Straw, 1996), but several studies have shown an immediate effect on height in the year of damage (e.g. Rook and Whyte, 1976; Britton, 1988). In these cases, defoliation occurred early in the year at the time of shoot extension. Consequently, the immediate response of height growth in Sitka spruce to spring/early summer infestation with *E. abietinum* suggests a strong influence on shoot growth at the time of infestation. Most needles attacked by *E. abietinum* do not fall until July, a month after peak infestation and after shoot extension is complete, and a proportion do not fall until the autumn (Straw *et al.*, 1998). This is too late to have an influence on leader growth in the current year. The decrease in height growth is more likely to be caused, therefore, by a direct effect of aphid feeding during the period of shoot development. Both Day and McClean (1991) and Straw *et al.* (1998) found that height increments in the season of infestation were more closely correlated with peak aphid densities than with subsequent needle loss. In contrast, stem diameter growth generally occurs later, in July and August, when aphid numbers have declined, and as a result may be less directly affected.

Evidence is emerging, therefore, that infestation by *E. abietinum* affects height and diameter increments in different ways. The aphid has a relatively large and immediate effect on height growth, probably because of a direct effect of aphid feeding, which is followed by a delayed effect on stem diameter and further effects on height increments, attributable to the loss of needles and comparable to the lagged response seen in other defoliator-tree systems. It appears that observations on height growth are not a good guide, therefore, to the effects of *E. abietinum* on stem diameter or volume.

Response of small and large trees

Estimates of the cumulative effect of *E. abietinum* on final tree size can only be obtained by using mathematical models to integrate the effects of successive aphid outbreaks over the life of the stand (Chapter 3). It is important in this process that the models describe the response of trees to defoliation accurately at all stages of the rotation. However, in Britain and Ireland, the oldest trees studied were 15 years old (Seaby and Mowat, 1993), whereas spruce stands are typically felled between 40 and 60 years. The stands investigated in Norway and Iceland were 26-37 years old at the time of defoliation, but it cannot be taken for granted that the response of trees in these climatic regions will be the same as in other countries. All detailed experimental work has been on trees <6 years old. Consequently, the impact of *E. abietinum* in the second half of the forest rotation is not represented by empirical studies in Britain and Ireland, and only by observational, tree ring studies elsewhere. Pole-sized or older trees might respond differently to infestation than young trees, hence calibrating models against current empirical data may misrepresent the true impact of *E. abietinum* during the latter half of the rotation and lead to inaccuracies in estimates of the effect on timber yields.

There are good reasons to suspect that older trees in plantations may suffer more from defoliation than young trees. Competitive interactions between trees in a closed stand are more intense than in pre-thicket crops, and the ability of trees to replace lost foliage is hindered once the canopy has closed. Young trees growing in open conditions produce new foliage almost exponentially in that the mass of new foliage greatly outweighs the mass of older needles by mid-summer. In Hafren Forest, current season growth formed 65-70% of total shoot length and total needles once it had developed (Straw *et al.*, 1998). Young trees can replace lost foliage quickly and are likely to recover faster. In a closed stand, canopy size remains more or less constant. As new foliage is produced, older foliage below is shaded out and dies. In these situations, different shoot cohorts make up more or less equal proportions of the total canopy and the current growth forms a relatively smaller proportion of the total (Straw and Fielding, unpublished). As a result, trees in the later stages of the rotation will not replace lost needles as quickly and the effects of defoliation will last for longer. Furthermore, the distribution pattern of aphids and needle loss in the canopy may differ between small and large trees, which may result in different responses to attack, especially in relative effects on height and diameter increment.

Comparisons between studies do not indicate any consistent differences in the response of small and large trees to infestation. The diameter growth of pole-sized trees in west Norway was reduced for a relatively long period, at least 7-8 years, but this followed 4 years of infestation. The severely defoliated trees at Hallormsstadur in Iceland showed reduced diameter increments for 2-4 years following two years of infestation, which is similar to the response of younger trees, but growth may have been declining on this site. It seems that the only reliable method of determining whether tree responses to infestation change over the life-time of a stand is, at some point, to attempt equivalent and comparable experimental studies on pole-sized trees growing under typical closed-canopy plantation conditions.

Influence of nutrient supply and atmospheric pollution

Even though research is limited, nutrient availability to Sitka spruce and atmospheric pollution appear capable of influencing the interaction between *E. abietinum* and its host-plant. Trees fertilised with higher rates of N or P had potentially faster growth rates than unfertilised trees, but they were also subject to higher rates of defoliation and suffered greater relative reductions in height increment (Seaby and Mowat, 1993). It is not clear, however, whether the increased attack outweighed the benefits of nutrient addition or whether, despite more intense defoliation, fertilized trees still achieved overall better height growth. Thomas and Miller (1994) found that fertilizer treatments applied at the time of infestation had no effect on defoliation rate, but may have helped to ameliorate the impact on diameter increment and speed tree recovery.

Higher rates of defoliation on fertilized trees suggests improved aphid development and reproduction on foliage that is richer in nitrogen or other nutrients, leading to higher aphid population densities. A similar effect appears to occur on trees fumigated with SO_2. Individual and population growth rates of *E. abietinum* were increased on plants exposed to elevated SO_2 concentrations (McNeill and Whittaker, 1990; Warrington and Whittaker, 1990). SO_2 had no direct effect on spruce growth at the raised, but realistic concentrations studied, but because the effect of the aphids was roughly proportional to their number, fumigation resulted in a greater impact on growth because of the higher populations of aphids generated. Other atmospheric pollutants might affect tree growth and aphid densities simultaneously, but for these and most other environmental factors, there is no information of how the impact of *E. abietinum* might be modified.

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Chapter 3

Growth costs to plantations: modelling the cumulative effect of defoliation by *Elatobium abietinum*

Timothy J. Randle and Anthony R. Ludlow

Summary

The process model GROMIT developed by the British Forestry Commission was used to simulate the long-term effects of periodic defoliation by *Elatobium abietinum* on Sitka spruce (*Picea sitchensis*). The model calculates total assimilation and allocates carbon according to the pipe-model to predict individual tree growth. Different age classes of foliage are incorporated, and all age classes except the most recent are allowed to be affected by defoliation. A brief description of the model is given, together with simulation results for defoliation rates of 0, 25%, 50%, 75% and 100%. Defoliation was set to recur every 6 years and stand development was simulated for 50 years.

Defoliation caused an immediate reduction in diameter increment of up to 40%. At the 100% defoliation rate, cumulative yield (stem mass) was reduced by 16% and absolute stem volume was reduced by 20% by the end of the simulation. As the trees became older and larger, recovery times increased. Light defoliation had little effect on long-term growth. Further simulations showed that single episodes of severe (100%) defoliation early in the rotation, at ages 6 and 12, had negligible effect on final yield.

Development of the model will require better parameterisation to describe spruce growth under different site and regional conditions, inclusion of within year susceptibility of tree growth to attack, and modifications to describe the distribution of defoliation within the crown in a more realistic manner. The model could then be used to predict the effects of different intensities, frequencies and durations of defoliation.

Background

Elatobium abietinum, the green spruce aphid infests spruce throughout northern Europe. Attacks by the aphid are sporadic, although serious infestation seems to occur every 3-6 years in Britain, often preceded by a year of less intensive infestation (Carter, 1977). Newly developed foliage is resistant to the aphid, while older needles are susceptible and can be highly defoliated.

The majority of spruce crops are grown for timber, although for some spruce there is a market for young trees, for example Norway spruce (*Picea abies*) Christmas trees. For timber crops, the main cause of concern following infestation is the potential for *E. abietinum* to reduce tree growth and hence yields, whereas for Christmas trees the main concern is the loss of needles and the adverse effect on physical appearance. Mathematical models that estimate cumulative effects on growth are more relevant to the former and models which indicate when attacks are likely to occur will be more important to the latter. This chapter considers the type of process model required to simulate the cumulative impact of repeated attacks on growth and describes some of the ways in which impact might be estimated.

The tendency for *E. abietinum* to affect only the older needles means that infestation rarely causes significant tree mortality (Bevan, 1966; Parry, 1976). This means that treatments to control the aphid are rarely applied, hence the importance of assessing cumulative effects on yield. Modelling is perhaps the only practical method for estimating cumulative effects, and models, especially process models, might also make it possible to address other questions. For example, is the timing of attack within the forestry-cycle critical, i.e. are young trees more or less able to recover after serious attacks than older trees? Is there an identifiable threshold of attack up to which trees may withstand defoliation without serious loss of production? To what extent are the frequency and duration of attacks crucial?

Empirical models are unable to answer such questions unless there is a large database of observations where infestation and yields have been categorised. Given the large set of combinations and permutations of timings, frequency and duration of attacks that are possible, such a set of data is unlikely to be obtainable in sufficient detail for such models to be developed. In contrast, models which are based on biological principles have much greater flexibility and may be better able to answer questions about the impact of defoliation on forest productivity.

Empirical models: yield tables

Yields from stands of mature trees are usually predicted by means of a yield table. These are empirical models, which take into account a range of management treatments, and they have been built up from many observations of real tree growth and yield. In Britain, these models are summarised in the Forestry Commission Yield Tables (Edwards and Christie, 1981).

The Forestry Commission yield tables are unusual in Europe because they do not use local vegetation or climate as a predictor of site quality. Instead, the tables for each spacing and thinning treatment consist of a family of curves, one for each yield class. The curve (yield class) appropriate to a particular site is specified by the dominant (top) height achieved by the stand by a specified age, e.g., 20 years. Given an initial planting density and typical management regime, the yield class gives an estimate of future production. This leads to a prediction of yield over years to come. The greatest return in terms of average volume per year occurs when harvesting is at the time of maximum mean annual increment. For Sitka spruce (*Picea sitchensis*) of yield class 14, with an initial spacing of 2.0 m and a management strategy of intermediate thinning, this would be at age 58 years.

If serious infestation by *E. abietinum* re-occurs approximately once every 6 years, then in the example above, the final crop trees could have been subject to 9-10 attacks. It is likely that this would have had an effect on the final crop yield. If height growth is reduced following infestation, then on subsequent visits, a lower yield class might be allocated to the stand as the top height-age relationship will have altered. It is possible that trees might regain their former vigour and even 'make good' single set-backs and return to their original yield class. However, without sufficient empirical data on the effects of defoliation, it is not possible to use such models to predict changes in growth patterns.

Why process models can help

Many organisations involved in commercial forestry and scientific research have developed what are termed 'process models'. Such models simulate the various biological, bio-chemical and physical processes that occur during tree growth. Some 'deep' models are very detailed in a few processes. Other 'broad' models have a wider range of processes simulated in less detail. The detail in which each process is simulated depends on the specific objectives of the model.

Because of the complexity of the processes involved in tree growth, and their interactions with the environment, no model is ideal (or is likely to be) for describing growth in all situations. In addition, many of the models are being developed further and alternatives are being explored. The ideal model for defoliation studies remains to be developed.

The process model developed by the authors has most of the necessary features for describing defoliation impacts on yield and has been used to produce some initial simulations of the effects of defoliation by *E. abietinum*. The structure of the model and the calculations it makes are explained in some detail in the technical description (Ludlow and Randle, 1991). A brief description of the model and some initial results are presented in the following sections.

The process model, GROMIT

Goals

GROMIT (GROwth Model for Individual Trees) was developed by the UK Forestry Commission originally to predict the effect of thinning and spacing on stand growth, as an aid to forest management. The aim was to develop a process model which simulated the parallel changes in volume, height and diameter growth during stand development. In particular, it was important that observed correlations between these variables were simulated accurately, even when spacing and growth rate changed.

Subsequently, with increased interest in the effects of climate change, GROMIT has been extended to incorporate hourly radiation and temperature data in calculating assimilation and maintenance respiration to allow prediction of the effects of increasing temperatures and CO_2. The model has been used successfully in an EC part-funded project, *Long-term effects of CO_2-increase and climate change on European forests (LTEEF)*, and is currently being used in another such project: *Predicted impacts of rising carbon dioxide and temperature on forests in Europe at stand scale (Ecocraft-II)*.

Place in the hierarchy of models

Because of the original aims, GROMIT is a detailed individual-tree model which can simulate growth of up to 144 neighbouring trees in parallel to represent a forest stand. A further 52 trees in surrounding 'guard' rows are also represented. Individual 'guard' trees differ in height, but each is proportional to the mean of the simulated trees. Growth is simulated from establishment (year 0) up to a stand age of 100 years. The interaction between neighbouring crowns is treated in detail and polygonal tiles are calculated following Nance *et al.*, 1987 to represent the area available to each tree and the projected crown area.

A pre-processor is used to calculate potential photosynthetic assimilation from hourly radiation and temperature data. Light interception is calculated using a version of the Lambert-Beer law which takes account of crown depth. Assimilation in each 'layer' of leaves is calculated separately from the radiation absorbed by that layer, subject to a saturating level. The output from this integration is the relationship between leaf area index (LAI) and potential assimilation over the year, and this relationship is input into the main model.

The trees are divided structurally into five compartments (foliage, branches, stem, transport roots and fine roots) and carbon available for growth is allocated to these compartments. Carbon available for growth is calculated as the difference between assimilation and maintenance respiration. Nutrients are not represented in the model, but the proportion of carbon allocated to fine roots is a parameter which can be altered to simulate the observed effect of site conditions on root-shoot ratio (McMurtrie and Wolf, 1983; Keyes and Grier, 1981).

After subtracting carbon lost in maintenance respiration, and the proportion allocated to fine-roots, the allocation of carbon between foliage and woody tissue is based on the pipe-model (Shinozaki *et al.*, 1964a, b). However, GROMIT allocates carbon to ensure that the area of *new* sapwood is proportional to the weight of *new* foliage (McWilliam, 1972; Ludlow and Atkinson, 1996). Other models relate *total* sapwood area to *total* foliage weight.

Annual cycle

GROMIT uses a variable-time-step integration routine to estimate annual growth increments. Seasonal or daily variation in growth patterns are not simulated during the run. In the pre-processor, photosynthesis is assumed not to occur when the temperature falls below a certain threshold (-5°C). All radiation data below this threshold are excluded. Radiation above the temperature threshold is divided into 10 classes and the gross assimilation rate (kg CO_2 m^{-2} ground area h^{-1}) is calculated for each of these radiation classes for different values of LAI, representing different numbers of layers of leaves. Assimilation is calculated using the mean radiation intensities in each radiation class and the number of hours in the year during which radiation at this intensity is observed. Assimilation is then summed across classes to give an annual value. These calculations are completed for each of a series of LAI values (1 to 10), and the values of annual assimilation obtained are used to produce a curve of gross assimilation rate against LAI (Figure 3.1) which is then used to parameterise the equation

$$P = P_0 \, (1 - e^{-k_2 L}) \qquad (1)$$

where P is the gross annual assimilation rate, P_0 is the rate that would be reached if all light were intercepted, L represents LAI and k_2 is a constant. P_0 and k_2 are input to the main model. (Note: k_2 is not a light extinction coefficient; it relates gross assimilation rate (instead of light interception) to LAI. A light extinction coefficient is used in the pre-processor to calculate radiation intensity reaching each of the layers of foliage).

A similar pre-processor calculates the effect of temperature on maintenance respiration of leaves, woody tissue and roots. Using pre-processors allows the model to take account of differences between sites in the annual pattern of radiation or temperature distribution.

Carbon flow

Potential photosynthesis calculated by the pre-processor is input into the main model as an annual value which may change from year to

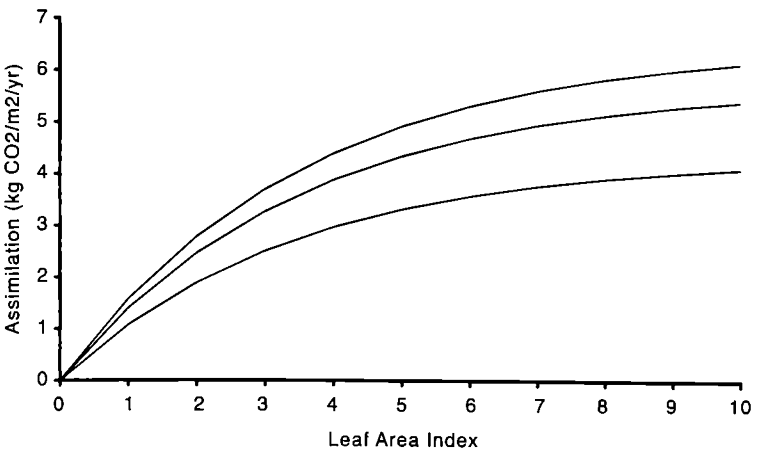

Figure 3.1 Curves derived from the preprocessor relating potential assimilation rate (per m^2 ground area) to LAI (equation 1). Hourly values of temperature and radiation intensity are from Jyvaskyla, Finland (62.24°N, 25.41°E). The three lines show the variation between different years; the best year, the worst and the average.

year of any simulation depending on variation in the hourly values of radiation and temperature.

1. Light interception in the preprocessor

Light interception does not include aspects such as leaf orientation, but allows for the fact that conical crowns have a higher surface area than their projected 'ground' area. This means that more of the foliage receives usable levels of diffuse light than would occur in a flat canopy. The assimilation rate is scaled appropriately to give output per square metre of projected ground area.

The separate interceptions of beam and diffuse radiation are calculated for each radiation class, but these are then added within the class before assimilation rate is calculated.

The model treats each crown separately and LAI is referred to the projected area of the crown rather than the total ground area. In other words, we use LAI to refer to the number of layers of foliage between the sky and the ground immediately below the crown. LAI is more normally used to refer to the number of layers of foliage between sky and ground for the whole stand, although in a closed canopy the two uses are the same.

The crowns are assumed to be conical and each portion of the crown of a single tree is treated as if it were a homogeneous canopy at an angle a to the vertical. This is best illustrated by considering LAI. LAI is useful when assuming a horizontally homogenous canopy but we use L_S which is the number of layers of foliage between the outside and the centre of the crown. For a conical crown with a half-crown angle a and using L for LAI.

$$L_S = L \sin a \qquad (2)$$

or, in terms of the exposed surface of the crown (C_S) and its projected area (C_P),

$$L_S = L \frac{C_P}{C_S} \qquad (3)$$

Since the crown surface is larger than the projected area of the crown, there is less light falling on it per square metre of crown surface. Hence diffuse light per square metre of crown surface is

$$I_{d,s} = I_{d,o} \sin a \qquad (4)$$

where $I_{d,o}$ is the diffuse radiation per square metre of ground area. Similarly, for direct (beam) light (I_b)

$$I_{b,s} = I_{b,o} \sin a \qquad (5)$$

Interception of diffuse light is calculated by finding the sphere integral for each layer of foliage between the crown surface and its centre. A horizontal surface receives light from the whole sky, but the side of a conical crown sees only a +90°. Since a is small (7.5°) we take half the usual sphere integral.

There are two problems in calculating the beam radiation reaching depth L_S. First, the path of the light depends on the solar angle. Second, the path is shortest on the side facing the sun, longest on the opposite side and intermediate in between. There is no need to know the suns' azimuth angle if the tree is circular, but we do need to take account of the different path lengths all the way round. This is done by dividing the tree into 20 sectors. The path of light to each foliage layer is calculated for each sector and photosynthesis of each sector is then calculated (taking account of diffuse light as well). Values of photosynthesis for each sector are then summed to give total assimilation per tree.

The total radiation was adjusted by sin a to allow for the ratio of crown surface area to crown projected area. This takes into account the fact that there is less light per square metre at the crown surface, but more square metres of surface. These effects do not cancel out because foliage is more evenly illuminated when it is spread over a larger area. As a result, little of the foliage is deeply shaded and total photosynthesis is greater.

The assimilation rate for a sector was calculated from

$$A = A_{max} (1 - e^{-EI/A_{max}}) \qquad (6)$$

where A is the assimilation rate (kg CO_2 m^{-2} leaf area h^{-1}), A_{max} is the maximum (gross) photosynthesis rate, E is the light use efficiency (kg CO_2 J^{-1}) and I is the photosynthetically active radiation absorbed. Note that dark respiration was not included in these calculations because its response to temperature is very different from that of photosynthesis and it was calculated by the maintenance-respiration pre-processor.

2. Assimilation rate in the main model

First, the number of layers of foliage per tree (LAI) is evaluated

$$L = \frac{W_f \sigma_f}{C_P} \qquad (7)$$

Where L is the LAI, W_f is the weight of foliage, σ_f is the specific leaf area of the foliage, C_P is the projected crown area of the tree.

The main model uses a modified version of equation (1) which incorporates C_P, to calculate assimilation rate per tree.

$$P_{tree} = P_0 C_p (1 - e^{-k_2 L}) \qquad (8)$$

Equation (8) allows automatically for gaps in the canopy both before canopy closure and as a result of thinning. It also provides a means of handling competition between trees, since the main effect of competition is to reduce each other's branch growth. The equation does not allow for shading by neighbouring trees, but this is likely to have only a small effect (Ludlow, Randle and Grace, 1990).

Respiration

Maintenance respiration is included as a temperature dependent function based on the relationship given by Korpilahti (1988). Annual maintenance respiration costs are subtracted from the carbon available for structural growth before allocation is calculated. The results are similar to the more familiar Q_{10} approach.

Growth respiration of each structural compartment (foliage, branches, etc.) is calculated by multiplying the compartment's growth rate by a constant. Hence, growth respiration represents a loss in efficiency of producing structural material.

Formation of tree structure: allocation

The carbon available for growth is the difference between income from assimilation and losses due to maintenance respiration. A fixed proportion of this is allocated to fine-root growth (η_r). The value of η_r tends to be site specific, having a higher value when site quality is poor (McMurtrie and Wolf, 1983).

The remaining carbon is allocated so that a given area of new sapwood is formed for each kg of new foliage. The model calculates the allocation to each compartment by the solution of a series of simultaneous equations. This ensures that there is a constant ratio between mass of new foliage and the conducting area of new tissue.

The ratio of new foliage to new sapwood area is different for stem, branch and coarse-root sapwood and is set by the parameters ψ_s, ψ_b, ψ_r, respectively. Measurements in the literature usually give the ratios of total sapwood area to total foliage (ϕ_s etc.), and some calculation is needed to find appropriate values for ψ_s, ψ_b, ψ_r. We assume a long-term equilibrium ratio, given estimated constant senescence rates for sapwood and needles, and by setting this ratio to the agreed value of ϕ_s solve for each of the parameters ψ_s, ψ_b and ψ_r. For example

$$\psi_s = \frac{\gamma_s}{\gamma_f \phi_s} \qquad (9)$$

Where γ_s represents senescence of stem sapwood and γ_f is the senescence rate of foliage.

Diameter increment is determined by the amount of new sapwood added to the stem.

Stand development

The model has been developed for Sitka spruce which has a regularly conical crown in plantations up to the normal felling age. In the model the crown angle may differ between trees but we assume that it remains the same throughout life for individual trees. We assume that branches from neighbouring trees cease to

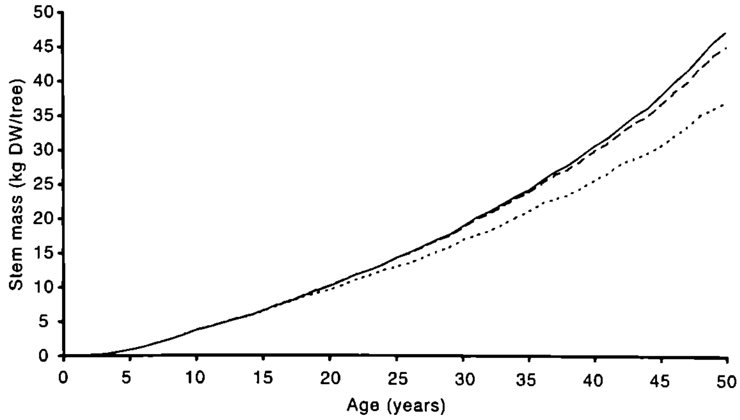

Figure 3.2 Effect of different defoliation intensities on stem mass of simulated Sitka spruce. Defoliation is of foliage over one year old and occurs every 6 years. ——, no defoliation; - - - - , 50% defoliation; ·······, 100% defoliation.

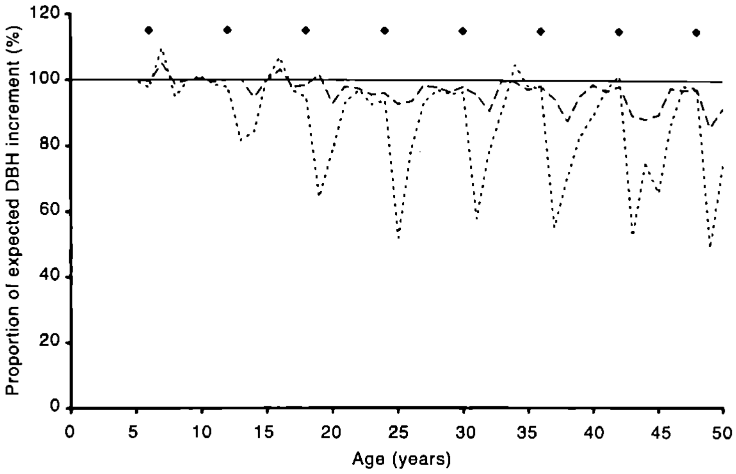

Figure 3.3 Effect of simulated defoliation on diameter increment of Sitka spruce. Growth is expressed as a proportion of the increment that would be expected if no defoliation had occurred. ——, no defoliation; - - - - , 50% defoliation; ·········, 100% defoliation. Years with defoliation are indicated by ◆.

grow when crowns touch. Competition between trees is calculated, therefore, by finding where neighbouring crowns intersect. This depends on the relative height of the trees, their distance apart and their crown angle.

In such a model, competition depends crucially on height growth. We calculate height growth as

$$H' = \frac{v_f N_f}{C_p} \tag{10}$$

where N_f is the rate of foliage production (kg DW yr^{-1}) and v_f is a constant giving the volume of new space occupied by each kg of new foliage. Although this value could be measured on real trees, there are no published data and we have had to estimate v_f rather crudely from related measurements.

Application of the model

Defoliation will reduce the amount of light intercepted by the crown and will reduce the number of sites where active photosynthesis may take place. To simulate the effects of defoliation by *E. abietinum*, the structure of the foliage compartment of the model was altered to incorporate foliage age classes. The foliage put on by the model each year was allocated to 'current needles', foliage remaining from the previous year was allocated to a second age class and so on until foliage was allocated to six age classes. (The final class contained foliage 5 years old and over.) Needle loss rates (γ_f) could vary from one age class to the next, but were set to be equal between all age classes for this simulation, with 23% of the foliage in one age class surviving into the next year for control simulations (Straw and Fielding, unpublished).

To simulate aphid attack the foliage mass in each of the age classes 2...6 was multiplied by a coefficient λ. This coefficient represented the proportion surviving attack so that in aphid-free years $\lambda = 1$ and when defoliation was complete $\lambda = 0$.

The simulated trees were grown from seedling size (28 cm height) to an age of 50 years, a nominal harvest date. In each simulation, the intensity of attack (i.e. percentage defoliation) was kept constant and attacks by *E. abietinum* were assumed to occur every six years. Only

Figure 3.4 Simulated effect of 0% (——) and 100% (- - - -) defoliation of older needles at ages 6 and 12 for Sitka spruce.

foliage greater than one year old was affected by an infestation. Simulations were run using 0%, 25%, 50%, 75% and 100% defoliation of older needles. To test if simulated trees could recover from a few attacks early in the rotation a simulation was run with 100% defoliation at age 6 and 12.

The weather data was allowed to vary from year to year (by using actual weather records), with no control being applied to stop 'good' or 'bad' years from following a simulated infestation. Meteorological data required for input by the model includes solar radiation, air temperature, humidity, precipitation and windspeed, although the models' sensitivity to windspeed is low, unless extreme conditions persist.

Outputs from the model can be numerous. We limit ourselves here to effects on increments in stem mass and diameter.

Results

Table 3.1 and Figure 3.2 show the effect of the cyclic defoliation on stem mass. It can be seen that after 50 years, there is little difference in stem mass between unaffected trees and those with a regular 25% defoliation. Trees which were subjected to 100% defoliation of older needles showed a marked reduction in stem mass.

Table 3.1 Effect of defoliation every six years on stem mass after 50 years in simulated Sitka spruce

Defoliation	Reduction in stem mass
0%	0%
25%	1.4%
50%	4.6%
75%	11.1%
100%	21.6%

Figure 3.3 shows the effect of different intensities of defoliation on diameter increment, expressed as a proportion of the increment expected from simulations with no defoliation. The immediate response to an attack was a loss in diameter increment, except that in the first attack diameter increment increased above that which would normally have been achieved (Figure 3.3). In older trees, there was a longer period of depressed growth than in younger trees.

Simulations of the cumulative effects of defoliation at ages 6 and 12 show that the simulated trees did indeed make up for their lost increment (Figure 3.4). It is not clear whether this was due to the timing of attack when the trees were juvenile, or because only two simulated attacks occurred.

Future directions

The initial results from the model simulations agree broadly with field observations. Diameter increments in the model were reduced by between 5-40%, which is similar to that observed in experimental studies (Chapter 2), and the period of depressed growth of 0-4 years is also comparable. However, over-shooting in diameter increments in young trees has not been observed in the field. This difference between the model and experimental results needs investigating. It is important that the simulation results from the model match the quantified observational data from experimental work and field studies on impact. Further parameterisation of the model for Norway and Sitka spruce, particularly to allow for site and geographical differences in tree growth and infestation, would perhaps improve the fit with empirical data and increase the flexibility of the model. Photosynthetic efficiency often decreases with needle age and this too may need to be measured and built into the model.

The model could be extended in two ways. The onset of budburst and budset changes the nutrient status of the host tree and these are known to have a significant effect on *E. abietinum* population dynamics and the damage caused (Day and Crute, 1990; Carter and Nichols, 1988). These aspects need to be incorporated if the model is to capture the tree's changing sensitivity to early or late attack within the year. Preliminary work has already been done as part of another EC-funded project: *Long-term effect of elevated CO_2 and climate change on European forests (LTEEF).*

A second extension to the model is needed to capture the spatial distribution of defoliation within the crown, and to simulate the effect that this might have on light interception and assimilation rate.

Another effect of damage by *E. abietinum* could be to disturb the relationship between sapwood area and foliage mass. Several process models are based on the pipe-model theory (Shinozaki *et al.*, 1964a, b) and assume a constant ratio between *total* sapwood area and *total* foliage biomass (e.g. Valentine, 1985; Mäkelä, 1986). This ratio is supported by Nikinmaa (1992) who also found that growth of the newest tree ring is related to changes in needle mass. In our model, the ratio of *new* foliage to *new* sapwood is assumed constant (McWilliam, 1972 reviewed by Ludlow and Atkinson, 1996). This approach allows an equilibrium state of *total* foliage:*total* sapwood to be achieved under constant conditions, but permitting disturbance of this ratio. Pruning experiments by Margolis *et al.*, (1995) on balsam fir (*Abies balsamea* (L.) Mill.) showed that severe defoliation (pruning) reduced sapwood area and increased heartwood, but the effect was not found after lighter pruning. The disturbance in *total* sapwood:*total* foliage ratio was still evident 2 years after pruning occurred. Further results from pruning/defoliation experiments may help to resolve the problem of modelling foliage: sapwood balance.

If the sensitivity of spruce to infestation by *E. abietinum* can be modelled successfully, then the model could be coupled with aphid population dynamics models to simulate the impact of populations that fluctuate more realistically in terms of the intensity, duration and frequency of attack. Predicted yield loss may be quantified in terms of reduced timber volumes and loss of direct revenue, or may lead to recommendations that harvesting should be delayed to compensate for the years of lost production.

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Chapter 4

Green spruce aphid population dynamics: effects of climate, weather and regulation

Keith R. Day and Neil A. C. Kidd

Summary

The within- and between-year dynamic relationships of spruce aphid populations in plantations of Sitka spruce are reviewed. Indices of aphid abundance have been obtained from suction trap catches and from forests, in the form of aphid counts on foliage. Correlations between trap and forest-based samples increase the confidence that can be placed in traps as a means of long-term aphid surveillance. The pattern of within-year aphid population change is determined by nutrient availability in spruce needles, whereas the timing of the population peak is governed regionally by thermal input. The size of the population peak (and the damage caused) is dependent on the population that survives the winter, and can be moderated by natural enemies. Simulation studies also confirm these conclusions and show how European regional differences in aphid population dynamics can be explained by the thermal environment. Year to year differences in population size (and the frequency of 'outbreaks') are determined by the severity of winter weather and feedback from the population density in the previous year.

Independent studies point compellingly to the role of (overcompensating) density dependence in this system. Various sources of density regulation are discussed. The available evidence suggests that the centrifugal redistribution of aphids (both apterae within trees and alatae between trees), especially adults at high population density, coupled with the loss of needle habitat, could explain much of the dynamic response observed. A growing understanding of spruce aphid population dynamics and the use of flexible simulation models will become useful tools in integrated pest management.

Introduction

The green spruce aphid *Elatobium abietinum* (Walker) shows wide variations in abundance at different times of the year, from one year to the next, and from one European region to another, even on one of its preferred hosts, Sitka spruce (*Picea sitchensis* (Bong.) Carr.). New foliage produced by trees in the year of damage is not severely attacked (Jackson and Dixon, 1997) and trees are rarely killed, so the aphid remains a perennial pest. Populations persist even on severely defoliated trees and continue to fluctuate within a plantation from the time of seedling establishment until the crop is felled.

'Outbreaks' are declared whenever mean aphid population density exceeds about 0.5 per needle, usually at the early summer aphid maximum. At such densities, aphids will generate noticable needle loss (Day and McClean, 1991 and Chapter 2). High populations of this order occur around once every 7 years in the British Isles (Figure 4.1, and Hanson, 1952) or perhaps 5-8 years in less favourable parts of the British Isles and more frequently in milder regions (Carter, 1995). The frequency of outbreaks is rather less in Denmark, but still irregular and clearly governed by weather (from year to year) and climate (from region to region) (Bejer-Petersen, 1962).

We review here what is understood of the ecological processes that are responsible for the population dynamics of this aphid. Weather and climate play an important, and sometimes dramatic role, but density dependence and the way in which it affects the rate of population change in consecutive years needs greater understanding in view of its significance to pest management intervention.

Density-related processes are commonplace in the population dynamics of tree-dwelling aphids (Dixon, 1990) but the functional relationships which give rise to such density dependence are often less well understood because of the

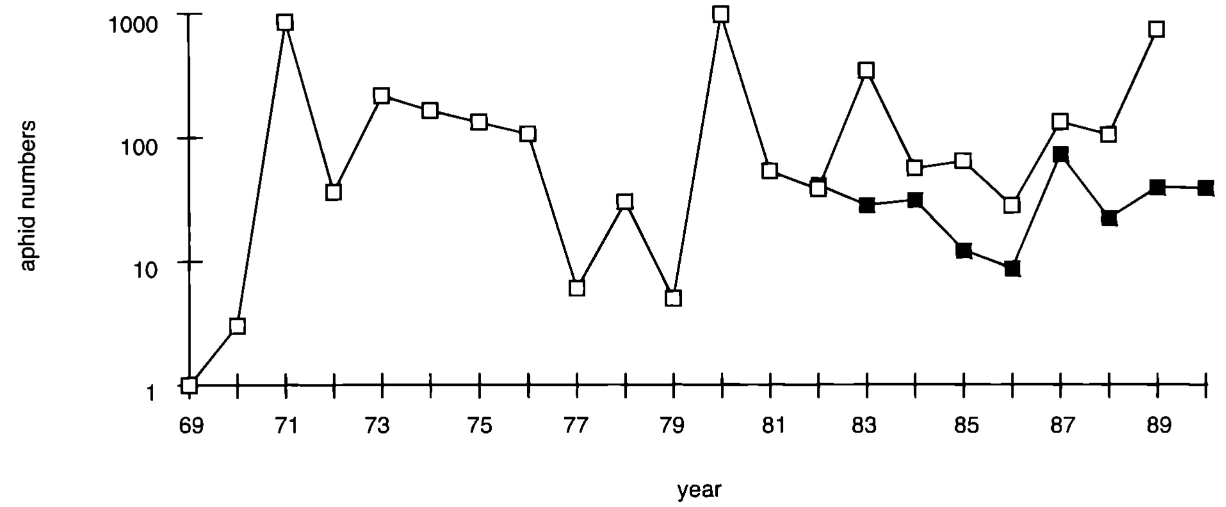

Figure 4.1 Total catch of spruce aphids from a suction trap each year at East Craigs, Scotland (☐ 1969-1989) as part of the Rothamsted Insect Survey (redrawn from Thacker, 1995) and estimates of population density (per 200 needle sample ■) in a Sitka spruce plantation at Clare Forest, Northern Ireland (1982-1990).

complex age and morph structure in aphid populations. Spruce aphid population changes in maritime parts of western Europe are particularly difficult to interpret because, unlike other tree-dwelling species, the aphid here has no egg stage forming a convenient end-of-season point of reference (Carter and Austarå, 1994). Growth and reproduction are possible year round. Nevertheless, it is becoming increasingly evident that population levels from year to year are, in part, a function of previous population densities.

With greater understanding of a species' population dynamics come opportunities to describe this in the form of general utility simulation models. There have been some successes in this direction (Crute and Day, 1990) but the time is now right to extend the approach to embrace a variety of pest management options, involving silviculture, resistance in the host plant and biological controls, whose efficacy can be tested using the simulation environment. We also show here how simple population models can help interpret population dynamics, in particular how they account for population patterns described in areas of Europe relatively new to the pest. We suggest that models of this type will provide the basis for a management tool in future.

Indices of aphid abundance

Absolute estimates of spruce aphid population density would be difficult to obtain and be of limited value in pest management. For this a knowledge of the abundance of the pest relative to that of its host plant is of prime concern. Nevertheless, a great deal has recently been deduced from the analysis of data obtained through the Rothamsted Insect Survey in Britain (Macaulay *et al.*, 1988). The spatial and temporal relationships between suction trap surveys of alate spruce aphids were investigated by Thacker (1995) and are reviewed elsewhere in this chapter. There are similarities between annual aphid population changes monitored by suction trap and field estimates of population size, even when the data from each arise from different parts of the British Isles (Figure 4.1).

A correlation has been found between suction trap catches and the extent of forest defoliation (the total area of forest damaged by spruce aphid in any year within 50 miles of a suction trap), which is an important confirmation of the accuracy of trapping and the first time such a relationship has been found for a non-arable crop aphid (Thacker, 1995). The aerial density of aphids (trap catch) was also related to the area of Sitka spruce in a region, a finding which suggests that suction traps will not be a particularly good way of comparing regional variation in aphid density on plant foliage (population intensity), unless a correction factor is used. It is the numbers of aphids present per unit of foliage, not the numbers present per volume of air, which determines the extent of damage and loss of tree growth potential. In addition, trap results in the west of Britain tend to be inherently less reliable than those in the east because the prevailing westerly winds mean there is less land area over which wind collects aphids in the west compared with the east (Thacker, 1995).

In conclusion, aerial survey suction traps are known to give a very good representation of general field population levels over a considerable area (Tatchell, 1991) and have provided data which will allow year to year comparisons of aphid populations reflecting the summer maximum in aphid population density (intensity) on forest trees, but spatial comparisons in trapping indices are probably less reliable, and should not be considered for long-distance regional studies.

Populations living on host plants can be evaluated in various ways and estimates obtained by stratified sampling. Samples have been stratified for height within canopy (Parry, 1969), canopy aspect (Carter, 1995), tree groups, or individual trees within a plantation compartment (Day, 1984a; Parry, 1974), for provenance within a randomised block design (Day, 1984b; Armour, 1996), and for forest plot or compartment (Powell and Parry, 1976). Many of theses studies have mentioned clear preferences for individual trees, making it a useful strategy to sample consecutively from marked trees. There has been no consensus on the way in which aphids are distributed within a tree, although various authors have mentioned a tendency for aphids to be relatively more abundant in different parts of the crown, and for there to be interaction with different stages of tree growth and at different times of the year. There is therefore no general prescription for sampling these aphids within canopies or for weighting sample number by stratum.

Several aphid population studies have been based on sample shoot excision (Day, 1984 a&b, 1986; Day and Crute, 1990; Parry, 1974). Samples of year *n*-1 age shoots were removed from the same trees at regular intervals through a season in year *n* (Day, 1984 a & b), or in the case of longer-term monitoring, once a year at the end of May when the population was known to be at its peak level (Day and Crute, 1990). Aphids were extracted by hand from the foliage, counted in the laboratory and assigned to seven growth stages and morphs. This enabled estimates to be made of recruitment rate from the ratio between adult aphids (virginoparae) present in the samples and the number of first instar aphids (Parry, 1974). The insects pass through the first instar in about a day in summer, so it is thought to be a good reflection of population fertility and anticipated population growth rate (Day, 1984a). Estimates of fecundity of virginoparae have been made by dissecting insects retrieved from field samples (Day, 1986). Similarly, estimates of the rate of production of alatae can also be derived from ratios of the various morphs in consecutive field samples (Day, 1986). Modified Tullgren funnels can be used for extracting aphids on shoots into 80% alchohol (Carter, 1995) and may be the best system for large numbers of samples requiring an estimate of total population, but could give biased results where conclusions are to be drawn from population morph structure since some aphids are more mobile than others (Day, 1986).

Moderately good estimates of population density (intensity, i.e. mean aphid number per 100 needles per sample) can be obtained with six random shoot samples per tree from within the mid two thirds of tree canopies. These would give coefficients of variation between 10-20% at most aphid population densities and nearer 10% for peak population densities around which most interest is focused (Day, 1995). Even this number of samples, taken repeatedly through a season and perhaps for several years, would be impractical for small trees. This problem has been resolved by Straw (personal communication) through repeated *in situ* aphid counts.

Seasonal patterns of population change - plant and aphid quality

In the British Isles and most other parts of Europe where the aphid has become a pest, the seasonal patterns of aphid abundance are characteristic (Parry, 1974 and Figure 4.2). Aphid numbers start to increase in March when temperatures exceed a developmental threshold of 4°C (Crute and Day,

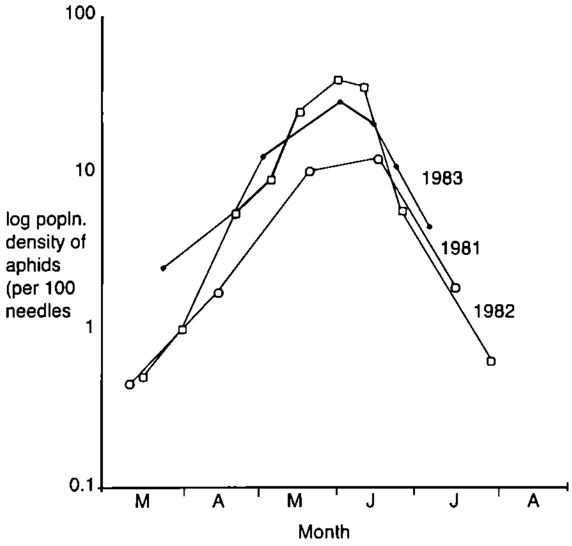

Figure 4.2 Mean population densities of spruce aphids estimated from foliage samples at Clare Forest, Northern Ireland (from Day, 1984a).

1990) and reach a peak towards the end of May (Day and Crute, 1990). Growth becomes exponential if weather is favourable in late spring and early summer (Figure 4.2) and the appearance of large populations of aphids on spruce foliage can be rapid and alarming for foresters even though the intrinsic rate of increase of this species (0.25 females female^{-1} day^{-1} at 20°C) is only a little above average for aphids in general (Dixon, 1985).

A decline in needle sap nutrient quality following bud-break (Carter, unpublished; Fisher and Dixon, 1986, their Figure 1a) results in the population falling to low levels again by the beginning of July (Day, 1984a) (Figure 4.2). Translation of these population trajectories to a physiological time scale removes the effect of ambient temperature on population growth in different years, but also shows that it is the timing of bud-break in any year which governs when the population is most likely to fall. It happens that in Northern Ireland this timing tends to be rather consistent from year to year (Day, 1984a) despite differences in spring temperature.

Milder winters and warmer springs will encourage faster population growth in anholocyclic aphids, but if these conditions are accompanied by an advance in foliar phenology and hence the manifestation of poor food quality, the potential increase in insect population density could be neutralised. Sitka spruce bud-break is determined as much by cold periods in winter as warm springs (Cannell and Smith, 1983), so generally warmer conditions advance the development of *Elatobium* while delaying bud-burst and maintaining favourable plant quality. Hence, maritime climates and greater global warming tend to favour the aphid pest during spring and early summer.

The peak in amino acid content of needles also coincides with the time at which there is the largest proportion of alatae amongst the offspring born to the spruce aphid (Fisher and Dixon, 1986). An increase in photoperiod is the main factor inducing the development of migrants, and host quality and aphid crowding modify the response (Fisher, 1982). There appear to be regional differences in the proportion of the population which enters the alate developmental pathway and hence the proportion of migrants. Although data from different sources are not strictly comparable, the proportion seems to be relatively low in Scotland (Parry, 1977), higher in Northern Ireland with a more distinctive maritime climate (Day, 1984a) where a maximum of 70% of the population became alate, and possibly higher in south-eastern England where the proportion of alates remained at or above 70% for nearly a month (Fisher and Dixon, 1986). If regional differences in migrant production are partly the result of heat input (Parry, 1978) and are phenologically determined by daylength, then spruce aphid populations in more northern countries such as Iceland may well be expected to respond differently from those in England.

Although the production of migrants has an important part to play in population dynamics, it is not the principal cause of population collapse at the beginning of June. Similarly, natural enemies have an important role to play and may determine the overall size of the population peak, but they do not represent the greatest influence on population collapse (Crute, 1990). The dramatic decline in population size results from a fall in fertility (Day 1984a; Parry, 1974; Parry and Powell, 1977) coupled with an increase in mortality and vagility-related losses of aphids from a tree (Day, 1986). Aphids become smaller (Thacker, 1995) and take longer to complete their development. Ultimately aphids suffer from declining nutrient availability, from loss of habitat as needles fall and possibly from competition among aphids for space. Parry (1974) and C. I. Carter (unpublished and reported in Fisher and Dixon, 1986) found a 50% decline of soluble nitrogen in needles from March to the end of July.

A very small number of aphids survive the summer, some perhaps on slightly better quality needles (Parry, 1979) or where they are able to avoid natural enemies (Crute, 1990). Populations start to build up in September in the UK (Straw, 1995) as a result of an improvement in sap quality following bud-set (Carter and Nichols, 1988). Defoliation can occur in November and December but such outbreaks are less common (Bevan and Carter, 1975; Carter, 1989). In summers with exceptionally hot and dry conditions, trees enter dormancy early thus providing aphids with longer opportunities for rapid development, particularly when the autumn itself is also mild.

Climate and weather

Several weather conditions affecting aphids have been mentioned. The most important of these occur during the winter months and govern annual changes in peak population density. The population of anholocyclic aphids which enters

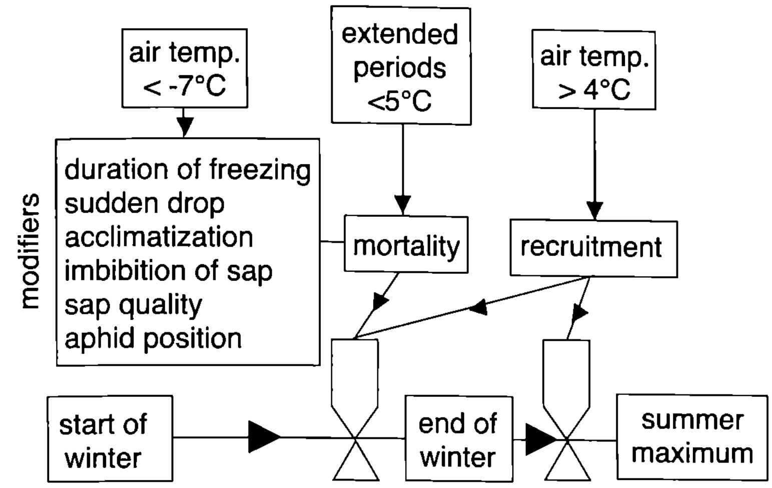

Figure 4.3 Relational diagram for populations of overwintering spruce aphids indicating main temperature-related constraints to population growth. Populations pass through winter and spring, eventually reaching a summer maximum for the year. Population growth (or decline) is influenced by key temperature variables acting on mortality and recruitment (redrawn from Day and Crute, 1990).

the winter will respond in a variety of ways to warmer or colder conditions (depending on the year or the locality) before population growth becomes exponential once more in the following April. In some cases the result will be a reduction in recruitment rate because development is slow, and in others there will be mortality (Figure 4.3). Some of the critical conditions for a range of European forests were analysed by Day and Crute (1990) following Bejer-Petersen (1962), Carter (1972), Ohnesorge (1961), Powell (1974), and Powell and Parry (1976).

The spruce aphid is a moderately chill-tolerant species (*sensu* Bale, 1993). That is to say, aphids may die as a result of low temperature before freezing takes place although many survive until the supercooling point is reached (Powell and Parry, 1976). The relative effects of different low temperature conditions during the winter and spring depend on climate and the geographical location. In coastal areas of Northern Ireland, where aphids experience a strongly maritime climate, the days when temperature drops below -5°C are relatively infrequent, and therefore the temperature above an aphid developmental threshold accumulated prior to bud-break is likely to be at least as important in setting the population peak in late spring (Day and Crute, 1990). Elsewhere, continental-type winters may override this effect and direct mortality from low temperatures may dominate.

Reliable aphid population data for several years at any locality could be interpreted solely in relation to climate and weather; winter temperature conditions explain a very high proportion of the annual variation in peak aphid population density, and are useful explanatory variables even where the aphid population data originates from suction traps (Thacker, 1995). However, a knowledge of temperature alone is insufficient to predict population trends since year to year change is also determined by overcompensating density dependence.

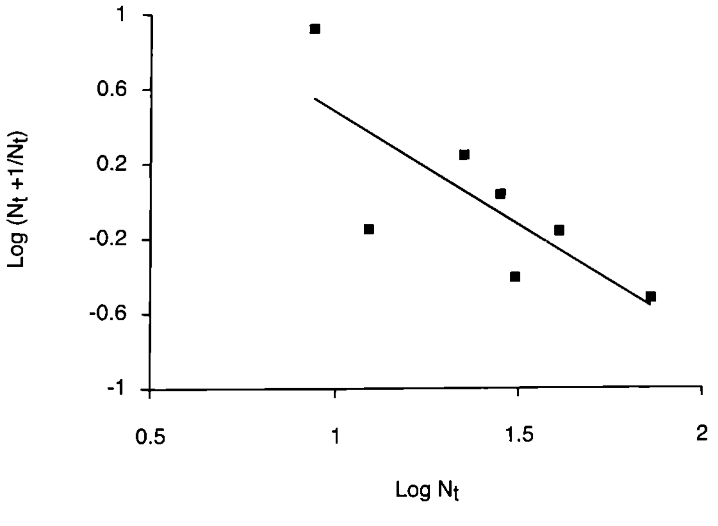

Figure 4.4 The relationship between the rate of population change and population density (per 100 needles) in consecutive years, based on estimates of maximum aphid population density in summer at Clare Forest, Northern Ireland (from Day and Crute, 1990).

Evidence for regulation

Population time series based on estimates of peak population in consecutive years give evidence of changes in numbers of the same order of magnitude (at least ten-fold changes are possible from one year to the next) (Figure 4.1). The population peak is of particular interest since it determines the level of foliar damage in a forest. The amplitude of the peak, varying from year to year, is partly determined by population in the previous year. There is an inverse relationship between the rate of population change between years (log $[N_{t+1} / N_t]$) and population density (log N_t) (Figure 4.4). This explains about 60% of the variation in population density and may comprise a number of processes acting on the population of aphids throughout the year, and whose joint effect is overcompensating density dependence (Day and Crute, 1990). The statistical validity of this relationship is dubious but there is some comfort in the knowledge that, although the axes are not strictly independent, more rigorous analyses of similar relationships in other aphids provide similarly significant results (Dixon, 1990; Wellings *et al.*, 1985)

The most exhaustive study of density dependence in spruce aphid time series has been based on the results of the Rothamsted suction trap data (Thacker, 1995). Convincing evidence of density dependence was obtained from time series at 15 sample sites representing the length and breadth of Britain and between 17-20 years. The result of density dependence is to reduce high populations within one year. 'Outbreaks' are consequently often preceded by low abundances of the aphid (Thacker, 1995) and even years with equitable winter weather can have low-level populations if they follow 'outbreaks' . Generally, a higher relative importance of density dependence at warmer sites means that populations here may be more stable than at those where winter temperature is more severe.

While the existence of density-related processes in the year to year dynamics of the spruce aphid is clear, the origin of such processes is less so. Plant quality often serves to mediate density dependence. Previous infestations of aphids may be deleterious to subsequent aphid development on conifers by inducing plant defences. This was found to be a possible source of cyclic population behaviour in the large pine aphid, *Cinara pinea* (Kidd, 1990). Defoliation of some conifers can result in marked (and delayed) feedback in the form of reduced plant quality for folivorous insects (Baltensweiler *et al.* 1977) but in others there appear to be no active induced defences (Larsson and Tenow, 1984). On the whole, the evidence for regulation by aphid-induced changes in host quality is weak for conifers and also for deciduous trees (Dixon, 1990).

Competition between aphids and reduction in aphid quality may conceivably play a role in density dependent population decline, but the evidence suggest that spruce aphids are not nutrient competitors, rather they benefit from the presence of other aphids since they are heavier when reared on chlorotic (previously infested) needles (Fisher, 1987). Infestation of aphids alters the amino acid balance of the needle sap to the advantage of other aphids, but competition does result if needles are shed prematurely and this in turn depends upon the level of aphid infestation (Chapter 2 and Day and McClean, 1991). The proximal cause of population change, however, is not aphid quality but mortality or dispersal.

The redistribution of aphids does not itself result in density dependent population change in a forest unless the potential of each disperser is not fully realised, perhaps because the act of dispersal reduces fertility and increases mortality. It seems that the fertility of dispersers is not reduced since the ratios of first instar nymphs to adults only makes sense if alates are included in the ratio (Day, 1984a). However, the loss of adults (apterae and alatae) while dispersing, may be an increased possibility with increasing density since dispersal of all morphs is strongly centrifugal and adults are more vagile than nymphs (Day, 1986).

A clue to the origin of density dependence may be in the scale at which it can be observed. Thacker (1995) examined the possible redistribution of population following the population peak by calculating b in Taylor's Power Law (Taylor, 1961) from the mean and variance of samples at different sampling scales. Values of b were calculated for samples based on needles, twigs and trees and any decrease in the value of b from before and after the peak population was taken to signify redistribution from high to low densities. Thacker (1995) found no evidence for spatial density dependence between trees or between needles, and although there was a significant redistribution between twigs, this did not amount to regulation of population between years. Initially the aphids are highly aggregated on certain twigs, and as the population decreases there is significantly less aggregation. In Thacker's study, between-tree movement had a lesser role in redistributing

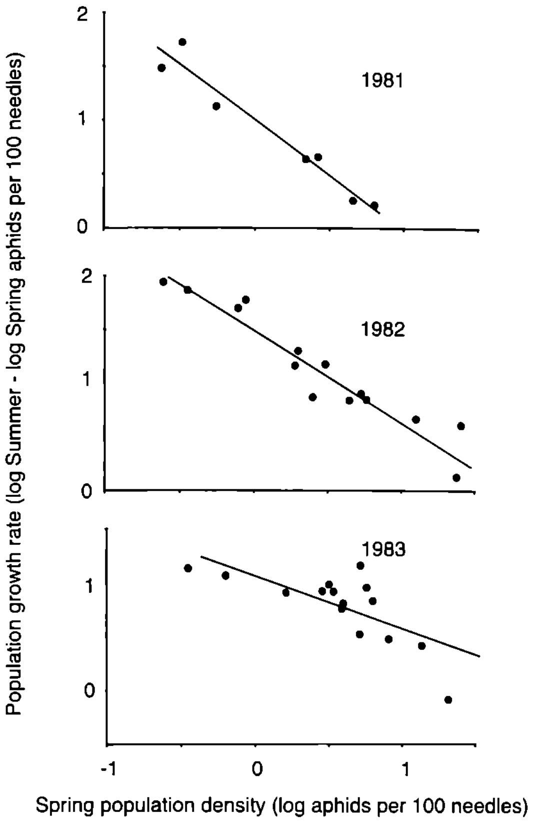

Figure 4.5 The inverse density dependence of spring aphid population growth rate on individual trees at Clare Forest, Northern Ireland (from Day, 1986)

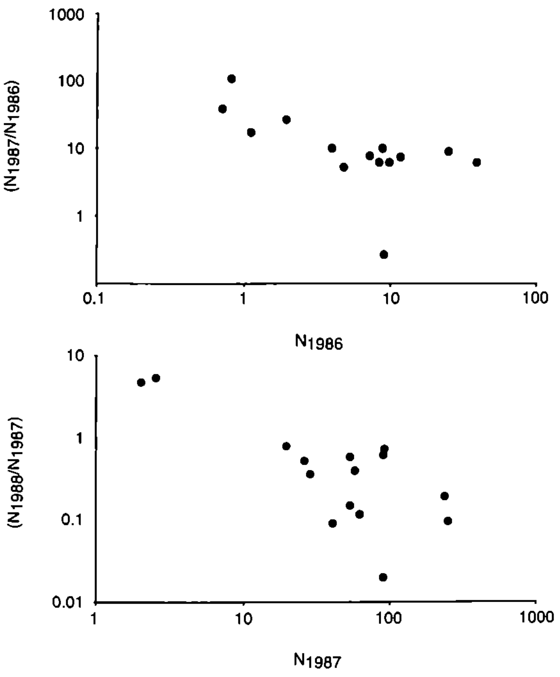

Figure 4.6 Peak aphid population density on individual trees plotted for consecutive years. The two years selected show a relationship with a slope below equality suggesting density dependent regulation at the tree level. The years illustrated are those with the most marked increase and decline in population overall (see Figure 4.1). Population estimates are based on aphids per 100 needles.

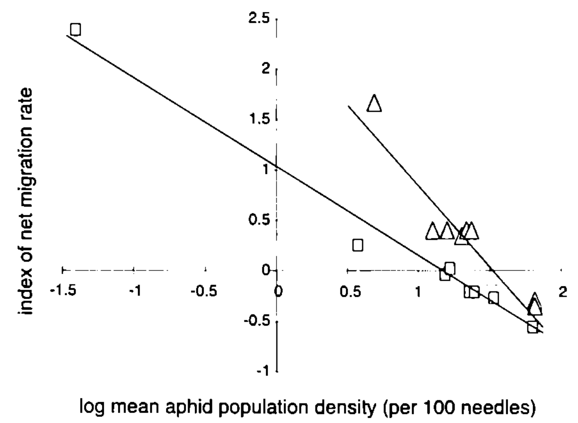

Figure 4.7 Changes in net migration rate (based on the relative production of alatoid instar IV nymphs and the subsequent occurrence on trees of alate virginoparae) in relation to initial (April) population densities of aphids estimated for trees at Clare Forest, Northern Ireland (from Day, 1986). Net migration in the current context represents either net immigration (gains) or net emmigration (losses). Symbols represent trees with different canopy types.

aphids than within-tree movement but overall there was little evidence that between year density dependence was the result of regulation at or below the scale of individual trees.

Maximum population density was in the region of 4-5 aphids per 100 needles in Thacker's study, whereas data reported by Day (1986) varied from a mean population peak of 8.7 in one year to 73.1 in the year of highest population (Figure 4.1). It is quite possible that detection of density dependence among sample units bearing low average aphid numbers (Thacker, 1995) might be more difficult. Certainly, density dependent population growth and decline in the same season has been observed between trees (Day, 1984a and Figure 4.5). As evidence for density dependence between years (t) at the level of trees, two plots of peak aphid populations (log [N_{t+1} / N_t] plotted against log N_t) are provided from an increasing and a declining population (Figure 4.6). Of the eight year to year comparisons between populations on individual trees which are possible with the data series, five strongly suggest density dependent population change similar to that in Figure 4.6.

Further evidence supporting density dependent redistribution between trees comes from a more detailed study of the dispersal of alate aphids. A distinction needs to be made between the production of alates which is density dependent (Day, 1984a; Thacker, 1995; Fisher and Dixon, 1986) and their redistribution between trees which is a function of flight (not all alates seem to migrate before larviposition). This was explored by reference to the relative numbers in field samples of immature and mature alate and apterous morphs (Day, 1986). The study showed that trees with low population densities of aphids gained relatively more alates than those with higher densities which show net losses (Figure 4.7). We conclude that the redistribution of aphids (within and between trees) and the gain or loss of individuals or their potential fertility may play a role in spruce aphid density regulation. The loss of needle habitat may be a compounding process and affect populations severely at the highest population densities which are only realised in 'outbreak' years.

Further population modelling

Most western-European populations of the spruce aphid correspond with the seasonal pattern of change indicated above, although some authors record a second peak population in autumn or early winter (Hanson, 1952; Hussey, 1952). In Iceland, however, the summer peak is smaller and later, with a fairly regular peak in late summer or early autumn. In terms of pest management, there is interest in what the effect of these differences might be on the host plant, and which extrinsic or intrinsic factors might be responsible for the different population behaviours. Candidate factors include (a) temperature (b) aphid life cycle (c) tree phenology and nutritional quality, and (d) natural enemies.

Lower temperatures in Iceland could contribute to greater winter mortality, and restrict population growth in the spring. A holocycle (Carter and Austarå, 1994) would minimise winter mortality but again restrict population growth rate in late spring. Low winter temperatures might be expected to advance budburst phenology and therefore restrict the period when high quality nutrients are available. Finally, lower incidence or absence of arthropod natural enemies may allow population growth later in the summer. Some of these ideas can be tested with relatively simple interactive computer modelling (Barlow and Dixon, 1980).

The model

Much of the fine detail that characterises real spruce aphid populations is absent from the computer model. The aim of the model is to capture the most essential features of the pest population, enough to reproduce the form of population trends and test the aforementioned ideas, but never complex enough to make high precision predictions of temporal abundance. Thus, day-degree developmental times and the pattern of reproduction of aphids are included in the model, while vital rates such as mortality and adult emigration are only included as approximations. This need not be a serious limitation, since the sensitivity of the model to variations in these approximate values can easily be tested.

The model is seeded by a small number of first instar aphids shortly after the beginning of the model year and reflects anholocyclic overwintering. The model also employs a simple overcompensated density dependent response to simulate adult emigration prior to reproduction, either by flight or otherwise. The equation describing density dependence is:

$$S = \exp(-C^{*}[N-T])$$

where S is daily survival of stage N, C is the density dependence coefficient and T the threshold above which density dependence comes into play. T is given as an arbitrary value of 200 throughout. Sensitivity analysis was used to see how critical the values for density dependence needed to be.

Reproduction of adults was accurately represented in the model using data from Crute (1990) and to simulate the summer decline in reproduction, brought about by changes in the nutritional quality of needles, the reproductive profile of adults was cut by two thirds after 500 day-degrees (approximately the end of June in Britain). This would be expected to capture any link with plant phenology. Mortality was characterised by an arbitrary 2% per day death rate on instars one and two. This version of the model, which was aimed at accounting for qualitative changes in patterns of aphid

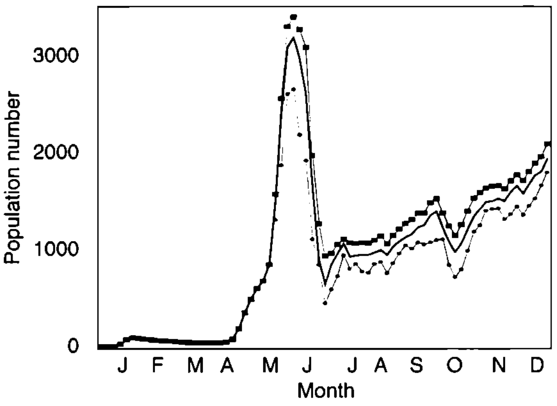

Figure 4.8 Simulation of British aphid populations in one year with density dependence coefficients of 0.5, 1 and 2.5.

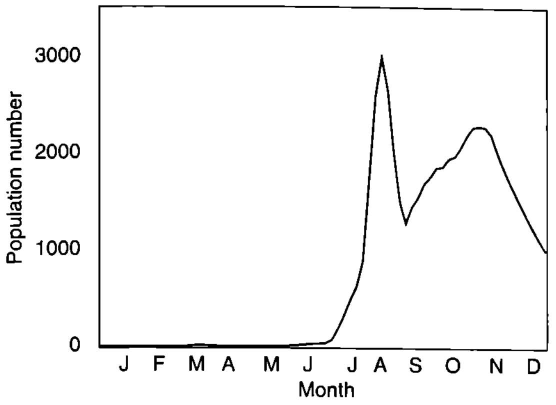

Figure 4.9 Simulation of Icelandic aphid populations in one year.

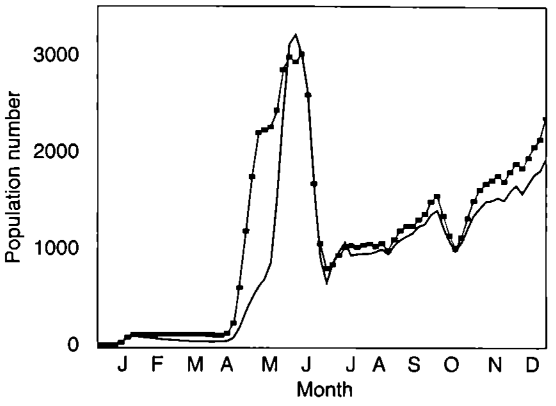

Figure 4.10 Simulation of British aphid populations in one year showing the effect of removal of background density-independent nymphal mortality.

dynamics, did not express population densities relative to units of plant habitat (e.g. the number of needles) but expressed population density as an arbitrary scale.

Results of modelling and sensitivity analyses

Predicted dynamics of the model corresponded quite well with the known pattern in Britain (Figure 4.8) although, without predators after the population crash in July, numbers continued to rise into the autumn. Using Icelandic field temperatures, the model predicted a later peak in aphid abundance in August (c.f. actual Iceland peaks in mid-July) and a second peak in autumn (Figure 4.9). The results are encouraging and suggest a dominant role for temperature in defining patterns of aphid population dynamics in Iceland.

The degree of density-dependence incorporated into the model did not appear to be particularly influential in determining the seasonal dynamic pattern. Only with very wide variations in the parameter value did dynamics change significantly (Figure 4.8). Similarly, removal of density-independent nymphal mortality made little difference to the shape of the seasonal trajectory (Figure 4.10). Finally, the model was very sensitive to the timing and age distribution of the seeded population at the start of a year. Delays to seeding (modelling holocyclicity, for example) or changing the population age structure, produced significant delays or advances in the timing of the peak, and in some cases, produced extra generations.

In conclusion the model lends support to the idea that temperature differences between Britain and Iceland can explain in large measure the different pattern of within-year population dynamics observed in these different regions.

Discussion

The accumulation of aphid population data from a range of sources has provided an opportunity to evaluate their relative merits. Samples of spruce foliage on which aphids are counted, give the most reliable estimates of population levels and enable detailed studies of processes governing population dynamics. On the other hand they are expensive to collect and necessarily limited to selected sites, and are difficult to justify for routine long-term monitoring or to provide pest management guidance. The correspondence between aphid counts in forests and suction trap catches, suggest that the latter would be useful as a regional tool and would provide information on long term trends. Comparison of widely separated trap catches is less reliable, partly because regions differ in the extent of Sitka spruce forest established.

Climate is of overriding importance to the spruce aphid, in determining range and abundance. Some sporadic occurrences of the aphid may appear anomalous (see Chapter 1) but most patterns are understood in the context of winter climate and weather and other thermal inputs which may influence the timing of periods of population increase and decline. These relationships can be characterised with simulation and multivariate models and the use of modelling should be extended as more reliable data on aphid abundance becomes available from additional European regions. Natural enemies are also important because it appears they may moderate the levels of abundance which aphid populations reach (Chapter 6) rather than change the fundamental pattern of population change during the year, which is more strongly determined by the nutrient flux in needle sap. Since foresters are more likely to be concerned with the size of population peaks (Chapters 2 and 3) rather than whether there is a peak or not, this makes natural enemies and their potential biocontrol a more appealing subject for further research.

Population data from quite independent sources confirms the existence of density dependent processes operating on spruce aphid populations between years. Other aphids on deciduous trees also experience overcompensating density dependence (Barlow and Dixon, 1980; Wellings *et al.*, 1985) but this occurs within years, whereas between year dynamics are governed by strong density dependence. Intraspecific competition operating through changes in aphid quality appears to be the main process responsible for regulation, together with additional effects of natural enemies (Dixon, 1990). So far we have no knowledge of annual differences in spruce aphid quality which could contribute to between-year density dependence, although aphid quality certainly changes dramatically within a year. Loss of needle habitat may play a part in regulation, particularly since the rate of needle loss is proportional to aphid density (Day and McClean, 1991) and it appears that some needles are lost even at low aphid population density (Chapter 2). It is noticable that adult aphids are particularly vagile (Day, 1986) and therefore could be expected to move from needles prior to abcission; the proximal cause of population change may therefore be starvation and losses of more mature aphids (with greater reproductive value) as they compete at ever higher population density. Aphids frequently undertake kinetic movements in response to the variable quality of the environment (Dixon, 1985) and these movements may involve aggregation or centrifugal dispersal in response to local resource status and the presence of other aphids. The evidence for density dependent redistribution of aphids is mixed. Thacker (1995) working with populations at low mean density was not able to confirm regulatory processes at the level of individual trees, whereas Day (1986) observed much clearer evidence for this in populations at higher mean densities. Population declines on all trees as sap quality deteriorates, but it is more marked on trees where population has reached a higher peak density.

Although the level of production of migrant alate aphids makes little contribution to seasonal decline in populations, there may be regional variations which require a better understanding in relation to thermal climate. The importance of migration is that it allows aphids to seek out foliar environments where conditions for some survivors may be marginally better than elsewhere. Determining the environmental conditions in a forest which allow survival during the summer is particularly perplexing because population density is so low (Parry, 1979; Thacker, 1995). Fisher and Dixon (1986) make the observation that a forest of Sitka spruce exhibits fairly synchronous bud burst and the quality of hosts during the limited period of aphid migration is correspondingly uniform, despite potentially different aphid population densities between trees. The aphid's migratory strategy is more likely to be successful in a forest of its (probable) natural host Norway spruce in which the timing of bud burst varies more and where migrating aphids might find trees which are both less heavily infested and of a better quality. Nevertheless, there are some well-studied plantation forests of young Sitka spruce where budburst differs on individual trees by up to one month (Straw, personal communication); under such conditions aphid populations should be expected to persist rather better.

The population dynamics of spruce aphids, although strongly affected by weather and climate, are equally strongly moderated by internal processes which encourage stability. Regions and climates with sporadically colder conditions could expect higher variability in population levels. Thacker (1995) suggests that populations should exhibit lower variability as mean temperatures increase. In a separate analysis of alate populations in Britain, Zhou *et al.* (1997) conclude that spruce aphid populations are characterised by 'noise muffling' - the effects of perturbation decay to zero over time, the system's intrinsic dynamics are predictable and any unpredictability is due solely to the direct effects of external noise. That is to say spruce aphid populations show little evidence for chaotic behaviour generated by endogenous processes.

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Chapter 5

A conspectus of potential natural enemies found in association with the green spruce aphid in north-west European spruce plantations

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Summary

An account is given of a three year survey of potential natural enemies of *Elatobium abietinum* from spruce plantations in Denmark, Great Britain, Iceland and Norway. Special emphasis was given to surveys of Sitka spruce plantations in Norway which has similar climatic conditions to that of Iceland. Some 28 species of Coleoptera; 6 species of Diptera; 6 species of Neuroptera; 5 species of Hemiptera; and 9 species of Araneida, all potential aphid predators, were found in association with *E. abietinum* during this study. Parasitoids and hyperparasitoids numbering seven species were reared from mummified *E. abietinum*. Six species of insect pathogenic fungi were found, five of which are newly recorded using *E. abietinum* as a host; only one species, *Neozygites fresenii*, was found in all four countries. The distribution of these natural enemies and their significance for regional differences in the development of *E. abietinum* populations is reviewed and discussed.

Introduction

Observations of natural enemies of the green spruce aphid, *Elatobium abietinum* Walker, have hitherto mainly concerned predators. A diverse fauna of mainly arthropod predators, but also bats and birds (Theobald, 1914; Hussey, 1952; Bejer-Petersen, 1960), have been recorded. It is generally accepted that coccinellids, hemerobiids and syrphids are the most important predators (Hussey, 1952; Börner and Heinze, 1957; von Scheller, 1958 and 1963; Ohnesorge, 1959; Bejer-Petersen, 1962; Crute and Day, 1990). Most attention has been given to the coccinellids, among which adults and larvae of *Aphidecta obliterata, Anatis ocellata, Coccinella 11-punctata, C. 7-punctata and Myzia oblongoguttata* have been specifically mentioned as very frequently occurring on Sitka spruce infested by *E. abietinum* (von Scheller, 1958; Bejer-Petersen, 1962). Spiders (Araneidae) have been considered as very likely contributors to aphid mortality due to high numbers of aphid cadavers observed in webs (von Scheller, 1958; Bejer-Petersen, 1962), but neither species nor quantifications of impact are given. Although birds may be of some importance, as they are the only active predators during the winter, their effect may not be entirely beneficial since they might select parasitized aphids which are more conspicuous (Hanson, 1951).

Records of parasitoids are much less frequent than records of predators. Hanson (1951) mentions the importance of parasitoids in controlling *E. abietinum* and Hussey (1952) observed up to 15% parasitism of *E. abietinum* populations during late summer. Other authors (von Scheller 1963; Parry 1969) report much lower values. Several hymenopteran parasitoids have emerged from mummies of *E. abietinum*; of these only a few have been identified: *Ephedrus koponeni* (Halme, 1992), *Lysaphidus schimitscheki* (von Scheller, 1963) and *Praon flavinode* (Fulmek cited in von Scheller, 1963).

There have been very few observations of pathogens on *E. abietinum*. Both von Scheller (1958) and Ohnesorge (1959) claim however that an unidentified fungal insect-pathogen, which they found on *E. abietinum*, reduced the population significantly. Only one species, *Entomophtora planchoniana*, has been recognized as a pathogen being able to cause substantial mortality within populations of *E. abietinum* (Day, 1984, 1986). According to these observations the fungus was found to be important quite early during the season, resulting in more than 12% mortality among the aphids.

Importance of natural enemies

The effect of natural enemies on the dynamics of anholocyclic populations of the green spruce aphid has been a subject of some controversy. In oceanic regions where this species can continue to breed throughout the winter, the resulting populations reach a peak in late spring/early summer (Carter and Cole, 1977; Day, 1984; Carter and Nichols, 1988; Crute and Day, 1990). After bud burst the numbers decline and stay at a low level throughout the growing season. This pattern of population development has been claimed to be due to changes in the nutritional value of the phloem sap and not caused by the effect of natural enemies (Parry, 1969, 1974, 1979). In earlier studies predators and parasitoids were considered to be the most important factor in the dynamics of the summer population of the aphid. Hussey (1952) found that aphid populations which were protected from predation increased during the summer, whereas unprotected populations decreased. As mentioned above, the importance of natural enemies has been emphasised by other authors (Hanson, 1951; von Scheller, 1958; Ohnesorge 1959) and biological control of *E. abietinum* by the coccinellid *Aphidecta obliterata* L. has been attempted (Schneider, 1966). There now seems little doubt that both host plant nutrition and natural enemies play significant roles in the seasonal and year to year population dynamics of the aphid (Chapters 4 and 6).

A different development of anholocyclic populations has been observed in Iceland where *E. abietinum* has recently been introduced; a population peak occurs in the autumn/early winter (Ottósson, 1985). Population peaks occur rarely in the autumn elsewhere, but Hanson (1951) observed an autumn peak in *E. abietinum* populations in England in 1950, after the predator populations had declined and Carter (1969) recorded a similar unchecked winter event in Scotland during exceptionally mild winter weather. Also from Denmark a few records exist of local defoliation due to the green spruce aphid in late autumn (1981 and 1993) (Harding, 1994; Harding and Carter, 1997). It is known that very few of the predators considered to be important to *E. abietinum* are found in Iceland (Olafsson, 1991; Agnarsson, 1996). Within the most important groups of predators (i.e. coccinellids, hemerobiids and syrphids) only four species are present in Iceland: *Syrphus ribesii, S. torvus, Parasyrphus tarsatus* and *Coccinella 11-punctata*; only one of them, *S. ribesii*, is common. As far as other predators are concerned, the carabid *Notiophilus biguttatus* is common and seven species of Empididae are present in the country. Several tree dwelling arachnids are present, some of them common (Agnarsson, 1996). Considering the parasitoids, two *Praon* species are present and *Aphelinus abdominalis* which is also known as a hyperparasitoid. The hyperparasitoids *Asaphes suspensus* and A. *vulgaris* are also present in Iceland.

Crute and Day (1990) have suggested that the development of populations in summer/autumn/winter cannot be explained exclusively by changes in the nutritional value of phloem sap and that it is modified by natural enemies. In a modelling experiment they found a similar population development to that of Iceland when certain predators (syrphids) were excluded from the model (these ideas are developed further in Chapter 6). It is therefore likely that the different natural enemy complexes in Iceland and in other regions may account for the dissimilarities in aphid population development.

Most observations of the natural enemies of *E. abietinum* have been made in Central Europe and only few records exist from the oceanic region of north-west Europe. Recognizing the need of reconsidering the importance of natural enemies, a survey of potential natural enemies of the green spruce aphid was conducted in 1993-95 in Norway, Denmark, Great Britain and Iceland. The aim of the study was to gain further information on natural enemies of *E. abietinum* in maritime north-west Europe with a special emphasis on areas in Norway which may later serve as a source for possible introductions of natural enemies to Iceland. A full description of this survey is given in Austarå *et al.* (1997)

Survey of natural enemies in maritime regions of north-west Europe 1993-95

The survey conducted in 1993-95 is the first and only comprehensive record of natural enemies focussing on their presence in anholocyclic populations. Predators and parasitoids were sampled in Norway and Great Britain; due to low spring and summer population levels in Iceland, sampling of predators was unsuccessful. Pathogens were sampled in all countries and diagnosed in Denmark.

In Norway and Britain samples of predators were taken randomly, at up to approximately 2 m height in the canopy, by beating branches over trays and by direct visual observations. In Norway sampling was done in plantations of *Picea sitchensis* and *P. lutzii* in 69 localities in June-August; the surveyed area extended from latitudes well south of, to well north, of Iceland (62°N-69°N) in order to cover the area of potential sources of natural introductions to Iceland. In Britain, 14 localities were sampled for natural enemies in both *P. abies* and *P. sitchensis* stands ranging from 51°N on the English-Welsh borders to 57°N in the Scottish Uplands.

Table 5.1a Potential invertebrate predators of *Elatobium abietinum* in maritime north-west Europe

Species	Recorded* during the study 1993-95	Earlier records
Coleoptera		
Coccinellidae		
Anatis ocellata	GB	a, f, g, h, i
Adalia 2-punctata	N, GB	b, j
A. 10-punctata	N, GB	e, i
Aphidecta obliterata	N, GB	a, b, e, f, g, h, i
Calvia quatuordecimpunctata	GB	
Coccinella 7-punctata	GB	a, f, h, i
C. 11-punctata		h, i
C hieroglyphica		b, e, i
Exochomus quadripustulatus	GB	
Myzia oblongoguttata		a, h, i
Propylea 14-punctata	GB	b, e, i
Scymnus abietis	GB	i
Cantharidae		
Cantharis decipiens	GB	d
C. livida		h
C. nigricans	GB	
C. obscura		h
C. pallida	GB	
C. robusta	GB	h
C. rufa	GB	
C. rustica		h
Malthodes fuscus	GB	
M. marginatus	GB	
Podabrus alpinus	GB	
Rhagonycha femoralis	GB	
R. lignosa	N	c
R. limbata	N	
R. testacea	GB	
Carabidae		
Dromius quadrinotata	GB	h
Notiophilus biguttatus	GB	h
Elateridae		
Agriotes pallidulus	GB	
Athous haemorrhoidales	GB	
Athous subfuscus	N	h
Denticollis linearis	GB	
Dolopius marginatus	GB	
Liotrichus affinis	N	
Selatosomus incanus	GB	

*Recorded in DK=Denmark, GB=Great Britain, Ic=Iceland, N=Norway, NI=Northern Ireland. All new records are given in Austarå *et al.* (1997).

a Bejer-Petersen (1962), b Börner and Heinze (1957), c Carter (1973), d Frazer (1988),e Hussey (1952), f Ohnesorge (1959), g Parry (1992), h von Scheller (1958), i von Scheller (1963), j Theobald (1914).

Sampling of *E. abietinum* for examination and diagnosis of insect pathogenic fungi in Norway was carried out simultaneously with sampling for predators and parasitoids. In Great Britain, aphids putatively infected by insect pathogenic fungi were collected during spring and in November from densely colonised trees in southern England and in Wales. In Iceland samples for pathogens were taken at 25 localities along the coast, of which 20 samples were taken during the autumn peak in October-December. The Danish samples were taken during spring and during an unusual autumn attack in 1993 in the north-west part of the country (Harding, 1994).

Populations of *E. abietinum* were generally low during the survey period. In Norway, *E. abietinum* was not found in several localities. The species recorded from Norway were thus not necessarily found with the aphid. In Britain, however, 1995 was a moderate outbreak year.

The natural enemies - predators, parasitoids and pathogens - that have been recorded on anholocyclic populations of *E. abietinum* in maritime regions of north-west Europe, are listed in Tables 5.1-5.3. The tables give a full record of the recent findings (Austarå *et al.*, 1997) together with old records. Only arthropod predators are included and vertebrate predators are omitted from Table 5.1.

Predators

Some 28 species of Coleoptera, 6 species of Diptera, 6 species of Neuroptera, 5 species of Hemiptera and 9 species of Araneidae, which are all potential aphid predators, were found in association with *E. abietinum* during the study 1993-95 (Tables 5.1a, 5.1b). Interestingly, only 6 species, the three coccinellids *C. 11-punctata*, *C. hieroglyphica* and *M. oblongoguttata*, and the three cantharids, *C. rustica*, *C. obscura* and *C. livida*, previously found in association with the green spruce aphid and generally considered to be important in regulating aphid numbers, were not encountered during the recent study. Of the 54 potential predators found, 12 have been

Table 5.1b Potential invertebrate predators of *Elatobium abietinum*

Species	Recorded* during the study 1993-95	Earlier records
Diptera		
Syrphidae		a, b, e, f, g, h, i
Melanostoma scalare	GB	
Episyrphus balteatus	GB	
Syrphus ribesii	GB, Ic	
S. torvus	N	
Parasyrphus sp.	N	
Empididae	N	l
Neuroptera		
Hemerobiidae		
Hemerobius atrifrons	N	
H. perelegans	N	
H. pini	N	
H. simulans	N	
H. stigma	N	b
Wesmaelius nervosus	N	
Hemiptera		
Anthocoridae		
Anthocoris nemorum	N	k
Miridae		
Psallus perrisi	GB	
P. varians	GB	
P. wagneri	GB	
Atractomus sp.	GB	
ARACHNIDA		i
Araneida		
Araneidae		
Meta segmentata	N	
Meta mengei	N	
Linyphiidae		
Drapestica socialis	GB	
Bolyphantes index	N	
Lepthyphantes tenuis	N	
L. obscurus	N	
Theridiidae		
Theridion sisyphium	GB	
Thomisidae		
Xysticus sp.	N	
Lycosidae	N	
Opiliones	GB	

* Recorded in DK=Denmark, GB=Great Britain, Ic=Iceland, N=Norway

a Bejer-Petersen (1962), b Börner and Heinze (1957), k Hodgson and Aveling (1988), e Hussey (1952), f Ohnesorge (1959), g Parry (1992), h von Scheller (1958), i von Scheller (1963), l Sunderland (1988).

mentioned specifically by other authors as predatory on *E. abietinum* the remainder are new records.

Table 5.2 Mummies, and parasitoids emerging from *Elatobium abietinum*

Species	Recorded* during the study 1993-95	Earlier records	Type*
Hymenoptera			
Aphidiidae			
Lysaphidus schimitscheki	N, GB	m, i	P
Praon sp.	N, GB	i	P
Aphelinidae		i	
Aphelinus abdominalis	N		P&H
Pteromalidae			
Asaphes suspensus	N	n	H
A. vulgaris	GB	h, i	H
Asaphes sp.	N	n	H
Coruna clavata	N	n	H
Mummies	N, Ic		

* Type: P = parasitoid, H = hyperparasitoid

m Mackauer and Starý (1967), f Ohnesorge (1959),
h von Scheller (1958), i von Scheller (1963), n Sullivan (1988).

Table 5.3 Insect pathogenic fungi isolated from *Elatobium abietinum*

Pathogen	Recorded* during the study	Earlier records
ZYGOMYCOTINA		
Entomophthorales		
Ancylistaceae		
Conidiobolus obscurus	GB	
C. coronatus	GB	
Entomophthoraceae		
Entomophthora planchoniana	DK	o, p
Erynia (=Pandora) neoaphidis	DK	
Neozygitaceae		
Neozygites fresenii	GB, DK, Ic, N	
Zoophthora phalloides	DK	

* Recorded in DK = Denmark, GB = Great Britain, Ic = Iceland, N = Norway

o Day (1984), p Day (1986).

The survey of predators was not planned in a way that makes it possible to exclude casual finds of predators from systematic presence or absence on trees infested or not infested with *E. abietinum*. No feeding experiments were undertaken and literature records are consequently used to evaluate the predator status of the sampled species.

Coccinellids are known to be important predators of *E. abietinum* (Börner and Heinze, 1957; von Scheller, 1958; Ohnesorge, 1959; Bejer-Petersen, 1962; Parry, 1992). Species previously observed in increased numbers on aphid infested trees were also recorded during the survey. Two coccinellids hitherto not connected with *E. abietinum* were found in Great Britain. In Norway, the three coccinellid species were found in various localities in 1993 on *Elatobium*-infested trees. In 1994 and 1995 no specimens were found in the more northern localities. However, in Norway *Aphidecta obliterata* has never been found north of 63°N, and the northernmost known records of *Adalia bipunctata* and *A. decempunctata* are from the eastern parts of Nord-Trøndelag county (about 64°N) (Vik, 1991).

Within the Cantharidae, several species are known to be aphid predators (Frazer, 1988). Von Scheller (1958) found 3 species commonly with *E. abietinum*, and *Rhagonycha lignosa* has been recorded in great numbers from *E. abietinum* attacked trees in Great Britain (Carter, 1973). *R. lignosa* and *R. limbata* were found in Norway on aphid infested trees; the former species is not known further north than about 63°N, but *R. limbata*, however, has been recorded even from Finnmark county (Vik, 1991). So, if *R. limbata* feeds on *E. abietinum*, low aphid population levels may be the reason why this species was not encountered during surveys in the northern localities.

In forests, aphids may form only a minor part of the diet of carabids (Sunderland, 1988). Only two species have been mentioned in relation to predation on *E. abietinum* (von Scheller, 1958). One of these, *Notiophilus biguttatus*, was frequently recorded from tree canopies during the survey in Great Britain. Elaterids are known to feed on lachnids on woody plants (Sunderland, 1988). The genus *Athous* is recognized to contain predators of *E. abietinum*, and A. *subfuscus* has been found feeding on *E. abietinum* (von Scheller, 1958). *A. subfuscus* was also found in Norway in 1993 and 1995, both years on trees infested by *E. abietinum.*

Among Syrphidae and Hemerobiidae there are also important predators of *E. abietinum* (Börner and Heinze, 1957; Hussey, 1952; von Scheller, 1958, 1963; Ohnesorge, 1959; Crute and Day, 1990), but although it is generally thought that syrphid larvae have an impact on *Elatobium* populations, no species had been identified until the three-year survey 1993-95. Also within the dipteran family Empididae there are predators of aphids living on forest trees (Sunderland, 1988). The unidentified adult species recorded was collected on trees with large numbers of *E. abietinum*, but without finding any Diptera larvae. Hemerobiids are among the very few predators whose quantitative effects on the population dynamics of *E. abietinum* have been subject of analysis (Crute and Day, 1990, c.f. Chapter 6). In Norway, hemerobiids were found during all three years both on infested and uninfested trees. Larvae of *Hemerobius atrifrons* were observed voraciously feeding on *E. abietinum* on trees in the field.

Anthocoris nemorum is considered an important predator of aphids (Hodgson and Aveling, 1988). This species was found in several localities on infested as well as on uninfested trees. Although no previous records exist connecting *A. nemorum* to *Elatobium*, it is reasonable to assume that it is a genuine predator of the green spruce aphid since it was found on trees infested by this aphid both in 1993 and 1995, and it has been regularly observed on aphid-infested spruce shoots in Northern Ireland (Day, personal communication).

Species within the spider families listed in Table 5.1b have been recorded as predators of aphids in forests (Sunderland, 1988). Von Scheller (1963) states that in an outbreak area of *E. abietinum*, large numbers of arachnids were present and contributed considerably to the reduction of aphid numbers. *Theridion sisyphium* makes effective webs across the spaces between shoots of thicket stage spruce and ensnares great numbers of alate aphids in early summer in Great Britain; *Drapestica socialis* makes no web, but hunts on the trunks of larger trees where it would encounter aphids on epicormic shoots.

Parasitoids

Most of the hymenopterous parasitoids were collected as mummies, the adults emerging in the laboratory (Table 5.2). Some of these turned out to be hyperparasites, among which *Asaphes* spp. and *Coruna clavata* (Sullivan, 1988) were found. *Aphelinus abdominalis* may act as a parasitoid as well as a hyperparasitoid. Species within Aphidiidae were recorded in Norway during all three years and the parasitoid *Lysaphidus schimitscheki*, which has previously been observed parasitizing *E. abietinum* in German populations (von Scheller, 1963; Mackauer and Starý, 1967), was identified in Norwegian and British populations. Others were found to belong to the parasitoid genus *Praon*. The specific *E. abietinum* parasitoid *Ephedrus koponeni* described from Finland (Halme, 1992) has surprisingly not been found in north-west Europe.

Pathogenic fungi

Until the recent investigation of natural enemies only one pathogen, *Entomophthora planchoniana*, had been documented from *E. abietinum*. During the survey another five species of insect pathogenic fungi, all from Zygomycotina: Entomophthorales, were isolated from *E. abietinum* (Table 5.3). *Neozygites fresenii* was found in all countries; in Norway and Iceland it was the only pathogen isolated. In Iceland, no infection was observed during the survey in spring 1994; during the autumn peak, infection levels varied between 0 and 19.8% in samples collected in October and November, whereas only two out of 3577 aphids sampled in December were infected. In Denmark and Wales quantitative studies showed that infection levels never exceeded a few percent.

The species *E. planchoniana, C. obscurus, N. fresenii* and *E. neoaphidis* represent the four species of insect pathogenic fungi which have often been documented as common pathogens on aphids in annual cropping systems (Papierok and Havukkala, 1986; Feng *et al.*, 1991; Keller, 1987; Keller, 1991; Balazy, 1993; Steenberg and Eilenberg, 1995). The composition of species is therefore similar to several other aphid-pathogen systems. *Z. phalloides* is also known from aphids, but is more rare (Keller, 1991). This species may be specifically adapted to a forest ecosystem. *C. coronatus* is a generalist among Entomophthorales isolated from a range of insect species (Balazy, 1993).

The apparent uneven distribution of the fungal pathogens in *E. abietinum* populations may reflect local variations in time and space rather than general regional trends. Each aphid pathogen may differ significantly in abundance between year and locality (Eilenberg *et al.*, unpublished). More detailed studies are needed to clarify how population dynamics between host and pathogen develop.

Concluding remarks

Although several observations exist of the activity of natural enemies and long lists can be elaborated of potential predators and of parasitoids and pathogens, the knowledge of the interactions between *E. abietinum* and its natural enemy complexes and the impact of these organisms on aphid numbers is extremely sparse. Much research is needed before even a vague picture emerges of the influence of predators and parasitoids in the regulation of *E. abietinum* populations (see Chapter 6). Also the influence of insect pathogenic fungi under different conditions and the possible interaction between *E abietinum,* its fungal pathogens and other tree-dwelling aphid species deserves further studies, e.g. to clarify if transmision of disease between aphid species takes place and if such transmissions are important for the development of epizootics.

Nevertheless, indications are given that specific natural enemies may under some circumstances aid in determining aphid numbers and the pattern of population development. Experimental evidence (Crute and Day, 1990) indicates that absence of certain predators may explain an autumn peak of *E. abietinum* populations as it is known in Iceland. Only a few of the natural enemies recorded in the three-year survey in maritime north-west Europe or earlier have been found in Iceland. The surveys thus indicate that several important natural enemies are absent, which may account for the difference in timing of aphid population development. The northerly coastal areas of Norway with a climate similar to that of Iceland, and with a richer fauna of natural enemies may however serve as a suitable source of possible introductions.

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Chapter 6

The quantitative impact of natural enemies and the prospect for biological control

Simon R. Leather and Neil A. C. Kidd

Summary

The arthropod natural enemies of the green spruce aphid are little known, rarely studied and poorly understood. The major groups identified in studies in Scotland, England, Northern Ireland, Germany and Denmark are the aphidophagous syrphids , lacewings and coccinellids. Parasitoids have also been recorded as causing some impact on aphid populations although recorded parasitism rates rarely exceed 10%.

The most commonly identified predator is the ladybird *Aphidecta obliterata*, although two other species have been found feeding on green spruce aphid, *Coccinella septempunctata* and *Adalia decempunctata*. Despite syrphids being poorly identified and possibly under-recorded, computer simulations indicated that they could be of use in reducing the numbers of the green spruce aphid. The possibility that host plant effects influence predator and parasitoid efficiency was considered.

A simple model to explore the possible role of predation in regulating the numbers of *E. abietinum* was developed and indicated that both coccinellid predators and hymenopteran parasitoids could play an important role in depressing aphid numbers.

Introduction

The green spruce aphid, *Elatobium abietinum* (Walker) (Homoptera: Aphididae), has long been regarded as the major aphid pest of spruce throughout Britain and Europe (Bevan, 1966). Its two main host plants in Britain and Europe are Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and Norway spruce (*Picea abies* (L.) Karst.).

Nymphs are produced all year round by both winged and wingless females (Hussey, 1952). Although the overwintering egg stage is seldom known to occur in Britain, *E. abietinum* is able to survive the winter period and continues to feed and reproduce parthenogenetically (Carter, 1971). In Denmark, the egg stage is rarely found and most aphids overwinter anholocyclically (Bejer-Petersen, 1962; Harding and Carter, 1997). As there are few or no natural enemies to feed on it during the winter, populations can build up rapidly at the onset of spring and usually reach a peak in the month of June (Parry, 1977; Dixon, 1985; Day, 1984). Outbreaks are most likely to occur after a mild winter (Bejer-Petersen 1962; Parry, 1969, Carter, 1971).

Several natural enemy species have been identified as possibly regulating numbers of *E. abietinum* but their effects have rarely been quantified (Leather and Owuor, 1996). For example, the summer decline in numbers of *E. abietinum* on spruce has been attributed to the action of natural enemies (Hussey, 1952) and the same natural enemies were reported to maintain the population at extremely low levels throughout the summer months until November when the population rose again due to a decline in natural enemy activity. Although it is now generally agreed that host plant nutrient availability governs the most significant seasonal changes in aphid numbers (Chapter 4), predators always have the capacity to determine the amplitude of seasonal population fluctuations (Day and Crute, 1990). Aphid specific predators such as coccinellids and syrphids have been identified as the most abundant group of natural enemies associated with *E. abietinum* (Bejer-Petersen, 1962).

In contrast to agricultural aphid species where a number of studies have been conducted on the role and nature of their natural enemies (e.g. Carter *et al.*, 1982; Leather *et al.*, 1984), few studies on the natural enemies of aphid pests of economically important trees have been reported. Studies on the natural enemies of some deciduous tree feeding aphids however, have been made in some detail (e.g. Dixon, 1970). Two notable exceptions are the pine aphid *Schizolachnus pineti* and the large pine aphid *Cinara pinea*, where the natural enemy complex is relatively well known (Kidd, 1982, 1990). Many of the predators are generalists but in the case of *S. pineti*, syrphids are regarded as being of great importance (Kidd, 1982).

The biology of *E. abietinum* is relatively well understood (Parry, 1969, 1976; Day, 1984, 1986; Fisher and Dixon, 1986; Fisher, 1987) and the effect of climate (Bejer-Petersen, 1962; Carter, 1971) and potential effects of climate change on this aphid have been discussed (Straw, 1995). However, information on the effects of natural enemies is very limited, even to the extent that many of the predatory species feeding on *E. abietinum* remain unidentified, or the quantitative effects of putative natural enemies are unknown (Chapter 5).

Assessment of natural enemy effects

In aphidophagous predators, enhanced reproduction can be of vital significance in their efficacy as in most cases the impact of these natural enemies is largely a result of the activity of the juvenile stages (Mills, 1982). Some authors believe that the numerical response is the most important component in the total response by natural enemies and is largely responsible for their regulatory effect (Rosen, 1985). It is thus surprising that in only two studies on the impact of predation on *E. abietinum* has this and the related variable, consumption rate, been measured (Crute and Day, 1990; Leather and Owuor, 1996). Without some idea of consumption rates by predators their potential impact is hard to determine.

Coccinellids

Aphidecta obliterata has been used previously as a biocontrol agent of *Adelges (Chermes) piceae* in the USA (Amman, 1966) and in Canada (Brown and Clark, 1959). It would thus have potential as a biological control agent of *E. abietinum*. Unfortunately reports of consumption rates by *A. obliterata* have not been reported. Parry (1992) compared *A. obliterata* feeding on *E. abietinum* with *A. obliterata* feeding on *Adelges cooleyi*, but unfortunately did not report consumption rates, instead he concentrated on physiological and physical characteristics of the coccinellids such as respiration rates and fat content.

The only study involving coccinellids that reports consumption rates and attempts to quantify the direct effects of predation rates on *E. abietinum* is a study of the two spot ladybird *Adalia bipunctata* predating *E. abietinum* feeding on Norway spruce (*Picea abies*) in England (Leather and Owuor, 1996). This study involved the use of sleeve cages and also laboratory studies to investigate consumption rates. The study which followed the populations of sleeved and unsleeved paired branches found that the only predator that occurred in any numbers was *Adalia bipunctata*. The study revealed that *A. bipunctata* had a functional response (feeding) that did not give a density dependent relationship. It nevertheless had a relatively strong numerical response both aggregative and reproductive, that tended to compensate for this. The regression analysis indicates that there was a direct link between the changes seen in the population growth index of the green spruce aphid and the abundance of feeding stages of the coccinellids (Figure 6.1) and that this fitted better if a time lag of one week was incorporated into the (data (Figure 6.1). In addition, there was a significant and negative relationship between the numbers of coccinellids present and the population growth index of the aphids (Figure 6.2).

Consumption rates of *Adalia bipunctata*

Experiments carried out at 20°C on each of four larval stages using *E. abietinum* as the food source, showed that on average it took 11 days to

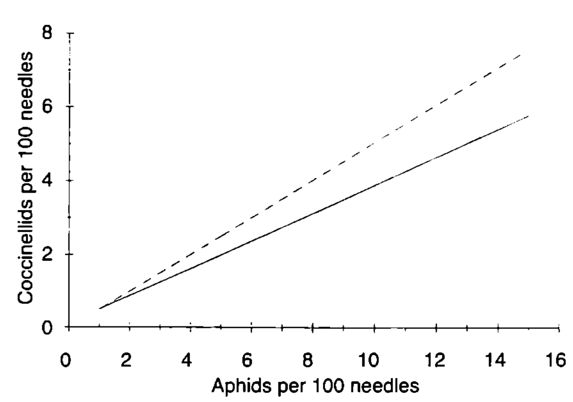

Figure 6.1 Relationship between number of coccinellid feeding stages present and number of *Elatobium abietinum* present on *Picea abies* trees without (—) and with (- - - -) a one week lag. y(no lag) = 0.38x + 0.085, r = 0.76, df = 10, $P < 0.001$; y (lag) = 0.51x - 0.036, r = 0.77, df = 9, $P < 0.001$. (Data from Leather and Owuor, 1996.)

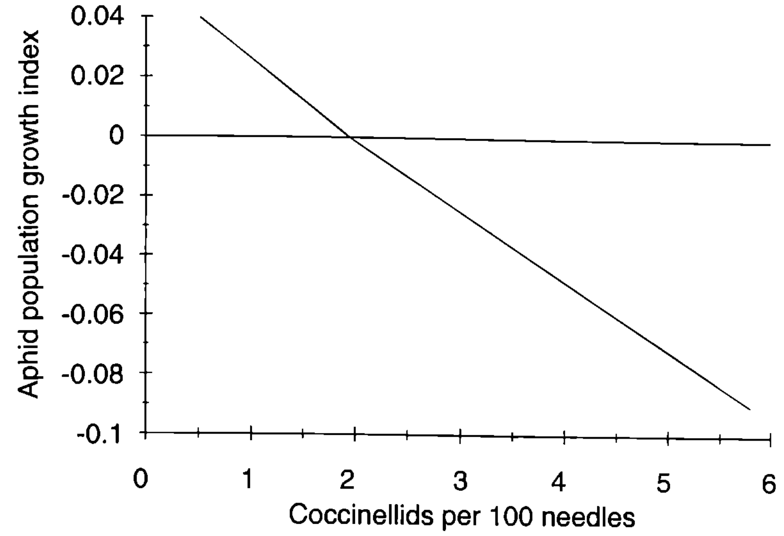

Figure 6.2 Relationship between number of coccinellid feeding stages per 100 needles and aphid population growth index. Lines calculated from Leather and Owuor (1996).

Table 6.1 Consumption rates of *Adalia bipunctata* when fed on *Elatobium abietinum* at 20°C (data from Owuor, 1993)

Predator instar	1st	2nd	3rd	4th
Number eaten	7.8 ± 1.3	24.4 ± 4.4	46.9 ± 10.4	192.5 ± 11.8
Proportion of total	2.9%	8.9%	17.3%	70.9%

go from the egg to the pupal stage (Owuor, 1993). The four larval instars took 2.1, 2.9, 2.1 and 3.9 days respectively. On average, to reach the pupal stage required the consumption of 271.2 aphids. The majority of aphids were consumed by the fourth instar larvae which accounted for almost 71% of the total (Table 6.1).

Searching behaviour

The searching behaviour of *A. bipunctata* on potted *P. abies* trees (c. 60 cm in height) was investigated in controlled laboratory conditions at 20°C and long day length (Owuor, 1993). Speed of movement and proportion of time spent searching branches for first, third and fourth instar larvae were investigated. The older larvae were more thorough in their search and spent more time searching on each branch visited (Table 6.2). All stages picked needles indiscriminately to begin searching, searched between two and five needles in a searching bout and then moved on unless an aphid was found. If an aphid was found the area was searched more intensively and needles were revisited and the number of needles searched in the locality rose to between 15 and 40.

Table 6.2 Searching behaviour of larvae of *Adalia bipunctata* on young *Picea abies* saplings at 20°C

Instar number	Speed of movement cm/min	Proportion of time spent on branches %
1	3.9	34
3	2.8	50
4	1.6	58

Table 6.3 Habitat preferences of the coccinellid species reported attacking *Elatobium abietinum* (after Majerus and Kearns, 1989)

Adalia decempunctata	Ten spot ladybird, hedgerows, woodland
Adalia bipunctata	Two spot ladybird, diverse
Aphidecta obliterata	Larch ladybird, conifer woodlands overwinters bark crevices
Anatis ocellata	Eyed ladybird, conifer woodland especially Scots pine, overwintering sites unknown
Coccinella septempunctata	Seven spot ladybird, diverse, overwinters in sheltered sites in aggregations
Exochomus 4-pustulatus	Pine ladybird, conifer woodland, sometimes deciduous, overwinters in bark crevices
Harmonia 4-punctata	Cream-streaked ladybird, conifer woodlands especially mature Scots pine, overwinters in bark crevices

Ladybird habitat preferences

When examining potential candidates for biocontrol roles it is important to ascertain the habitat preferences of the organism in question. Of the coccinellids most commonly reported attacking *E. abietinum*, four can be classified as conifer specialists, although in all cases *Pinus*

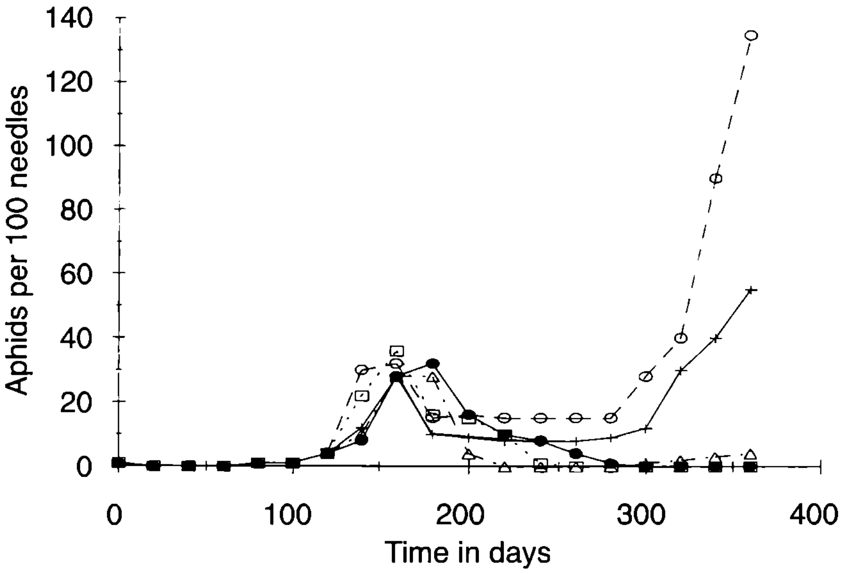

Figure 6.3 Effects of predators on the population development of *Elatobium abietinum*. Data from Crute and Day (1990). Field results (●), model results with syrphids and hemerobiids (△), model results with no predators (○), model results with syrphids only (□), model results with hemerobiids only (+).

sylvestris is cited as the most preferred habitat (Table 6.3); one, *A. decempunctata*, is most commonly found associated with hedgerows and woodlands, implying a preference for deciduous trees and the other two species are reported as being found in a wide variety of habitats.

Hemerobiids

Hemerobiids have been reported in a number of studies (Chapter 5), but only one species has been identified specifically, *Hemerobius micans*, and only one study has attempted to assess the impact of hemerobiids on populations of *E. abietinum* (Crute and Day, 1990). Hemerobiid larvae were more common in the upper parts of Sitka spruce crowns and rarest in the lower parts of the crown. The experiments reported looked at the effects of temperature on the consumption rate of aphids by *H. micans* over a series of four hour periods. No information on either the instar of the prey or the predator was available. The number of aphids consumed per four hour period ranged from 3.5 at 12°C to 9 at 24°C, although consumption rates levelled off at 17°C. Using these data in a simulation model Crute and Day (1990) were able to show that hemerobids were unlikely to have a significant effect on numbers of *E. abietinum* in Northern Ireland (Figure 6.3)

Syrphids

Syrphid larvae, although frequently recorded as feeding on *E. abietinum* (Chapter 5) have received very little attention, both in terms of

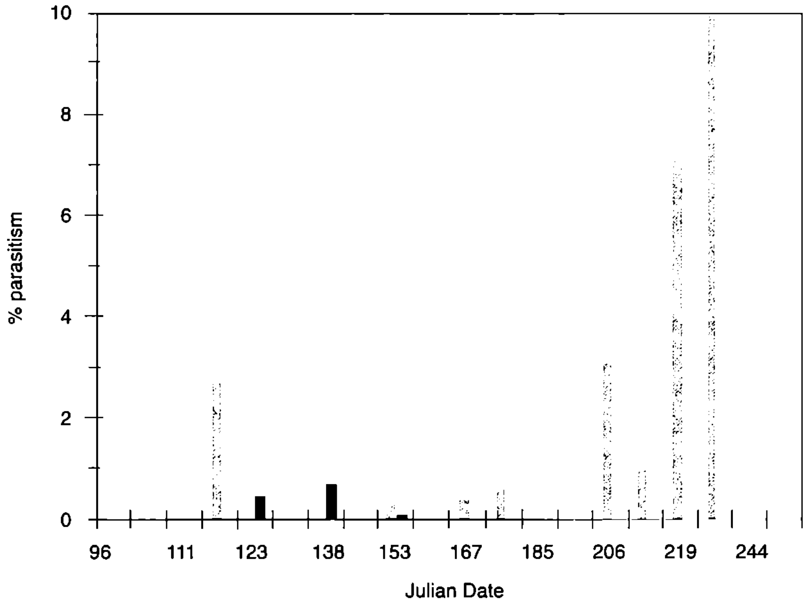

Figure 6.4 Parasitism rates of *Elatobium abietinum* in Scotland at a high density (■) and low density (■) site. Data from Parry (1969).

identification and in assessing consumption rates. Only one study has examined the feeding rates of syrphids associated with *E. abietinum* and this only examined the effects of temperature rather than instar and functional responses. As with the hemerobiids, consumption was measured over six temperatures on non-specified instars of prey and predator. Consumption rates ranged from just under three aphids per 4 hour period at 12°C to just under five aphids per 4 period at 24°C. The consumption curve levelled off at 17°C. Using the same model as discussed earlier, Crute and Day (1990) were able to show that syrphid larvae had a significant effect on numbers of *E. abietinum* (Figure 6.3), and in fact suggested that it is the effect of syrphid larvae that keeps *E. abietinum* numbers at their characteristic low levels throughout the summer.

Parasitoids

Parasitoids, although recorded in a number of studies, do not appear to have a large impact in those cases where their numbers have been recorded (Parry, 1969). Using data from Parry (1969) it was possible to calculate the impact of parasitoids on a high and low population of *E. abietinum* in Scotland in one year (Figure 6.4). Parasitism rates never exceeded 1% in the high population, although in the low population a parasitism rate of just over 10% occurred, but this coincided with the alate migration period.

The model

The aim of this project was to produce a model of predation which could be incorporated into the generalised spruce aphid model (Day and Kidd, 1998) to assess a) the predator contribution to observed aphid dynamics in the field and b) the possible opportunities for manipulation through biological control.

To this end the model had to be able to:

1. make full use of available data on consumption rates and searching behaviour of predators and
2. be sufficiently simple to construct/program without sacrificing realism.

On the second point it must be recognised that insect predation is a complex process and previous simulation models have failed through trying to incorporate too many components, becoming unwieldy, difficult to parameterize and ultimately impossible for others to understand. It is thus essential to capture the essence of the predation process without getting embroiled in fine detail.

The simplest route to achieve these aims was to modify the existing age-structured, Nicholson-Bailey type parasitoid model, which was already part of the POPULA computer simulation model package developed by Kidd and his associates at Cardiff (unpublished). The parasitoid model works by having daily age groups divided into two stages (Table 6.4a). Where events are influenced by temperature, the age categories shown in Table 6.4a are day-degrees rather than days. Adults search at random as defined by the Nicholson-Bailey equation (single searching coefficient *a*), and encounters with hosts each result in an oviposition event. These are gathered up and put in age group 1 at the end of each day.

To use this model structure for an insect predator, assume the parasitoid immature stage as being equivalent to the predator egg stage and the parasitoid adult as the larval and adult predators (Table 6.4b). For simplicity, we can ignore the pupal stage but it is easy enough to insert this stage between larvae and adults. The larval stage corresponds effectively to a *pre-reproductive*

Table 6.4

a) Age structure of the parasitoid population in the model. The number of age groups in each stage is variable, depending on species. In this illustration immature development is 10 days and adult development 8 days

[---------------------------Immatures---------------------------] [----------------------Adults----------------------]

Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
No.	5	5									10	10	10	10	10	10	10	10

b) Age structure of the predator population in the model. Again, the number of age groups in each stage is variable, depending on species

[------------Eggs------------] [------------Larvae------------] [----------------------Adults----------------------]

Age	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
No.	5	5									10	10	10	10	10	10	10	10

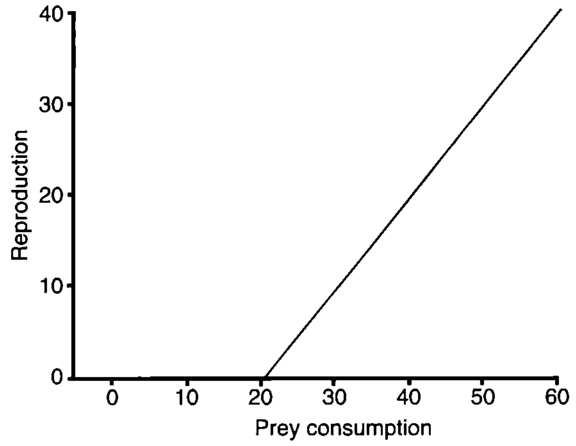

Figure 6.5a The relationship between the number of prey consumed per predator and the resulting number of predator eggs laid, as predicted by the model of Beddington *et al.*, 1976.

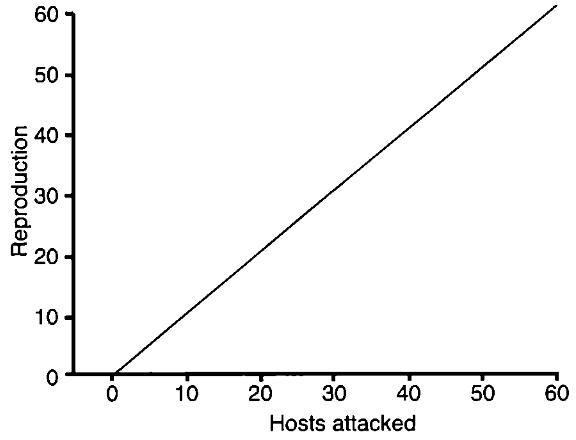

Figure 6.5b The relationship between the number of hosts parasitised and the resulting number of adult parasitoids emerging, as predicted by the Nicholson-Bailey model.

adult stage in the parasitoid. The only difference with the parasitoid model so far is that searching is defined by two coefficients, one for larvae (*a*) and one for adults (*b*). In the model predator larvae and adults were both assumed to live for a maximum of 20 days.

Reproduction can easily be catered for in this model by using the Beddington, Free and Lawton (1976) model, which defines the relationship between food consumption and reproduction as a linear one with a reproduction threshold caused by the need for some food to be diverted to maintenance (Figure 6.5a). When food consumption falls below a certain value, reproduction stops. The Nicholson-Bailey parasitoid equivalent (Figure 6.5b) has instead a perfect equality between consumption and reproduction, being a special case of the predator model. It is very easy now to link food encounter rate, as defined by the search coefficient *b*, to predator daily reproduction, assuming no delay in converting food to eggs. The likely delay (measurable in the laboratory) can however, be easily incorporated into the age structure of the model, by inserting the required number of age groups at the start, in front of the eggs. These correspond to embryonic egg development.

The only significant component now missing from the predator model is the effect of prey availability on larval survival. On average 271 aphids are required to complete larval development in *A. bipunctata.* It is fair to assume then, that if this number of prey is not encountered by each predator during larval life then the predator dies before reaching adulthood. This corresponds to an average daily requirement (for the 6 days of larval life in the theoretical example (Table 6.4)) of 45 aphids. In the model, if the daily encounter/capture rate (assuming all encounters result in successful capture) falls below 45 aphids per larva, then that cohort of larvae is eliminated.

The advantage of this predator model is that it can easily be constructed from the parasitoid version. In fact, the parasitoid model becomes a special case of the generalised predator model. The model is parameterised as follows:

- two searching encounters (larval and adult) involving random search
- two reproduction parameters (slope coefficient and constant)
- interval between food consumption and resulting reproduction
- prey requirement for completion of development
- age boundary between larvae and adults (when non-reproducing 'parasitoids' start to reproduce).

Parameter values for all of these components should be fairly easy to obtain from simple laboratory and field experiments. Some in fact are already known for *A. bipunctata.* The model itself has already been modified to take account of these new components and using theoretical data it is possible to show the kind of result that emerges.

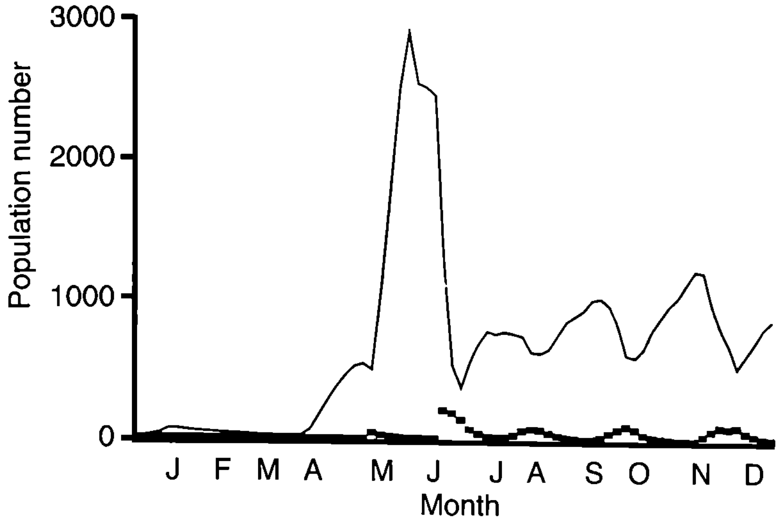

Figure 6.6 Simulation of spruce aphid and predator numbers using aphid/weather information relating to Chapter 4, Figure 4.8 and predator information given in the text. 50 predators, all female introduced on 10 May, with searching efficiencies a=0.002, b=0.004.

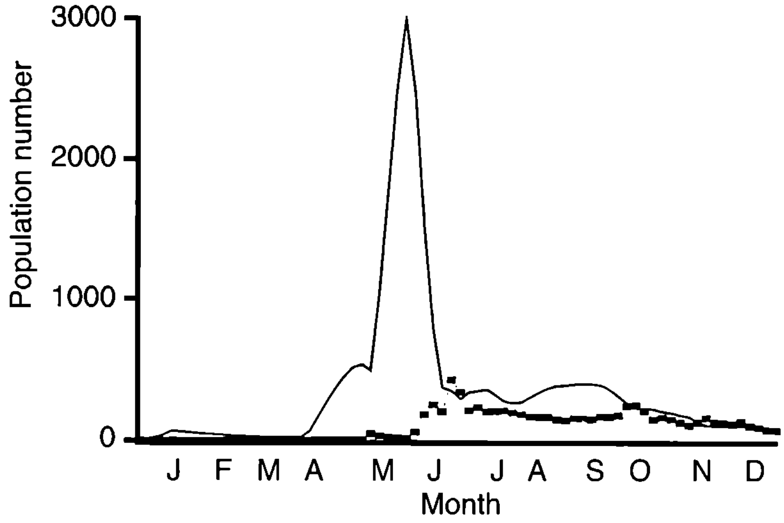

Figure 6.7 Simulation of spruce aphid and parasitoid numbers using aphid/weather information relating to Chapter 4, Figure 4.8 and parasitoid information given in the text. 50 parasitoids, all female introduced on 10 May, with searching efficiencies a=0.003.

In the model adult predators are introduced at specific dates during the year. This is really for use in biocontrol introductions, but it does allow flexibility in trying out potential dates for the appearance of natural field populations of predators. With an introduction date for predators of 10 May and using 1986 temperatures for South Wales the picture that emerges is shown in Figure 6.6. The aphid peak is reduced, but numbers fluctuate as each generation of predators appears in the summer. This in itself does not mean much, but the comparison with the parasitoid situation is instructive.

The corresponding situation for a parasitoid with the same life history characteristics as the predator, i.e. immature development time the same as predator egg development time (50 day-degrees in the model), and adult parasitoid life span the same as larval plus adult predator life span (40 days) is shown in Figure 6.7. Here, the depression in the aphid peak is similar, but the residual summer aphid population is lower with no fluctuations. This shows the effect of having all adults reproducing, as opposed to having a cohort non-reproducing (i.e. the predator larvae). Also, the delay in turning food into reproduction with reduced efficiency, is enough to induce the cycles in the predator, while absent in the parasitoid.

These tentative simulations do no more than show the possibilities that the model provides to tackle important questions about spruce aphid predation. The next stage is to collate all the relevant information on spruce aphid predation to determine what extra information needs to be obtained from experimental work. This, in conjunction with the new model opens exciting possibilities for testing spruce-aphid-predator interactions.

Discussion

Several contradicting views have been put forward concerning the role of natural enemies in the regulation of populations of *E. abietinum*. Hussey (1952) and Crute and Day (1990) were of the opinion that natural enemies had an important role to play in maintaining low summer aphid population, but Parry (1969) could find no real proof of this, being of the opinion that the change was brought about by a density-dependent change in the host quality. Severe infestations of *E. abietinum* have been reported to result in heavy defoliation of spruce and thus a reduction in food available to the aphid and this in turn led to increased aphid mortality due to starvation (Bejer-Petersen, 1962). It has also been suggested that the reduction in the number of needles caused by aphid defoliation increases the efficiency of searching by natural enemies as they were left with fewer needles on which to search (Bejer-Petersen, 1962).

Aphid specific predators, i.e. coccinellids and syrphids, appear to play the greatest role in aphid population regulation and one attempt at biological control with *Aphidecta obliterata* has been tried (Schneider, 1966). General agents, e.g. spiders, appear to play only a minor role. Coccinellid adults hibernate as adults and become active early in spring; syrphids on the other hand hibernate as fully grown larvae and do not appear to feed in spring. Ladybird beetles are therefore more likely to influence the spring population of the aphids. The effects of ladybird predation may be further affected by the location of the trees and perhaps even the species. The conifer specialists may be fine tuned to *Pinus sylvestris* sites and find spruce sites less attractive, either because of ground vegetation effects, spruce sites tending to have a less diverse herb layer, or because overwintering sites may be less readily available on spruce trees due to differences in bark structure. Parasitoids attacking the pine beauty moth first locate their host by selecting the tree that they expect to find their prey on, and consequently non-native trees are not found as often by the parasitoids as native trees (Leather and Aegerter, 1998). This may apply equally to predators and parasites of *E. abietinum*. Non-conifer specialists, e.g. *A. bipunctata*, may only have an effect on aphid populations on trees that are either not in plantations, e.g. park trees, or only occur in plantations that are close to agricultural land or with a significant number of broadleaved species present.

Future research

It is apparent that data are needed in a number of areas to understand more fully the dynamic interactions between natural enemies and the green spruce aphid throughout its range. The following areas require detailed research:

- identification of predator complexes in different geographical regions and in different types of plantation
- identification of specific predators and parasitoids associated with *E. abietinum*
- consumption rates of the specific predators need to be determined
- more experimental studies using cages / sleeves in the field
- identification of possible plant effects on host location by predators, e.g. Sitka *v* Norway.

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Chapter 7

Selecting for resistance in genetically defined Sitka spruce

Susanne Harding, Keith R. Day and Hazel L. Armour

Summary

Current tree breeding programmes in Sitka spruce aim at improving adaptability, quality and yield and so far do not include resistance to the green spruce aphid. The processes involved in the resistance mechanisms are not fully understood. Indications are given of the importance of secondary compounds and other hypotheses focus on the availability of sap nutrients. Also non-chemical features related to needle structure may be relevant. Differential susceptibility to attacks by the green spruce aphid has not only been demonstrated between spruce species, but also at provenance, family and clonal level. Provenance tests in Northern Ireland have shown significant variation in aphid peak population density between provenances and, although somewhat contradictory, correlations between population density and the original latitude of the seed origin. No influence of latitude was found in Danish trials. Within-provenance variation is very profound, making selection of resistant plant material possible in most provenances, a circumstance which gives excellent prospects for tree improvement programmes. Also at family level, significant differences in susceptibility to the green spruce aphid have been evidenced. The family heritability is high and high gains can be expected from selection. Resistance is obviously inherited by the offspring and appears to be fairly consistent in time; resistance has been demonstrated in offspring more than 30 years after selection for the trait. Examples of significant variation at clonal level are given. It is concluded that the advantages of including aphid resistance in current breeding programmes of Sitka spruce are obvious.

Introduction

The extent of genetic variation in Sitka spruce makes it a suitable candidate for tree breeding programmes (Fletcher, 1992). The current programmes of work with this species are aimed at improving the adaptability, yield, quality and economic return of forest planting stock (Brandt, 1970; Lee, 1986a,b; Roulund, 1974, 1990). It is estimated that the potential gain from currently available seed in the UK will be a minimum of 15% for height at 10 years, which should realise a similar increase in volume at rotation age (Lee, 1990, 1992). Further gains are expected once superior full-sib families have been identified using tested specific cross-pollinations and cutting propagated clones (Lee, 1986c, 1992; Costa e Silva *et al.*, 1994; Jensen *et al.*, 1996; Nielsen and Roulund, 1996).

The green spruce aphid is an economically important pest of the European Sitka spruce stands and serious attacks occur regularly in areas with a mild winter climate, where development is anholocyclic and winter survival may be high, i.e. in the atlantic regions of north-west Europe (Chapters 1 and 4). Nevertheless, the green spruce aphid has hitherto been regarded as a tolerable, or unavoidable, component of the tree production system and no systematic account has been taken of the potential for resistance in current breeding stock. The aphid, however, together with all other normal environmental variables, is implicitly taken into account since the gains are based on field-trialled and unprotected trees. As the European forest industry moves closer to a reliance on genetically-improved Sitka spruce, there are opportunities to evaluate the relationship between these trees and the way in which populations of aphids develop and cause damage.

Host tree species of the green spruce aphid are restricted to the genus *Picea* (Hanson, 1952). Feeding may seldom occur on other conifer species, but is of no importance (Furniss and Carolin, 1977; Blackman and Eastop, 1994). Some spruce species become severely discoloured upon aphid infestation and readily shed their needles whereas other species suffer only slightly from attacks or are not infested at all. The green spruce aphid is not only harmful to Sitka spruce; it has a pest status in the production of Norway spruce for Christmas trees in Britain and in some Central European countries, and in the growing of spruce species cultivated for ornamental purposes, in particular blue spruce, *P. pungens*. Furthermore, shelterbelts of white spruce, which has been a significant element of the landscape in some regions, have been fatally damaged and white spruce seed orchards in British Columbia are frequently defoliated (Rene Alfaro, personal communication).

Ultimately it would be both useful and ecologically interesting to understand the nature of the resistance mechanism in terms of the processes involved. A starting point is the knowledge that not all species of spruce are equally susceptible to attack by the green spruce aphid. Species differences were observed already by Cunliffe (1921), Dumbleton (1932), Fox-Wilson (1948) and Hanson (1952) but systematic investigations by Nichols (1987) clearly demonstrated that the aphid attains higher densities and has a better performance on North American species like Sitka spruce, white spruce and blue spruce than on most European and Asian species. In field observations she found all North American species but one to support high aphid population levels, comparable densities being obtained only on the West Chinese *P. asperata*. Interestingly, this species is considered to be only distantly related to Sitka spruce (Roulund, 1969). These findings were confirmed in laboratory experiments where the green spruce aphid had the highest mean relative growth rate (MRGR) and a higher final weight when feeding on the North American spruces and on *P. asperata*. Of the Eurasian species, Norway spruce resulted in MRGRs comparable with those recorded on Sitka spruce.

No unequivocal explanation to this intra-generic variation in susceptibility to the green spruce aphid has been given. Dumbleton (1932) suggested the species differences were due to differences in cell-sap composition and results by Nichols (1984) indicate that the foliage of less-favoured spruces, typically Eurasian and Asian species, contains a number of secondary compounds (phenolics and terpenoids) which are lacking in the susceptible North American species. Plant phenology, however, appeared not to be related to differences in aphid performance. Another indication of the importance of secondary chemistry in aphid/spruce interactions is given by Jackson and Dixon (1996). It has been known for some time that aphids avoid new foliage, preferring to feed on the foliage from previous years' growth until foliar maturation (Parry, 1976). Only recently has this preference been attributed to volatile substances in the epicuticular wax of new needles (Jackson and Dixon, 1996). The aphid clearly uses the epicuticular wax to distinguish between needles of different ages. Epicuticular waxes trap and concentrate plant volatile compounds such as monoterpenes which are known to occur in high concentrations in young needles (Hruitford *et al.*, 1974). The volatiles seem to act at a distance and reduce the survival of aphids, and aphids confined to new foliage were observed not to feed and were very active (Jackson and Dixon, 1996). However, on *P. pungens* spruce aphid populations may feed and propagate on the new foliage as early as about 6 weeks after budburst (Harding, unpublished)

Also, it is known that the nutrients in spruce needle sap have a dramatic effect on aphid populations during a growth season (Chapter 4). If the availability of primary nutrients varies between spruce origins, then this too could result in apparently different aphid attack rates, and would probably be observed by differences in aphid population growth rates at periods when nutrient levels were highest (spring and autumn). Another mechanism could be through differential winter survival on trees with different needle supercooling ability (Powell and Parry, 1976). This idea has not since been tested with a range of Sitka spruce origins, although at the time Powell and Parry (1976) could not relate relative susceptibility or resistance to provenance.

Non-chemical features may also be relevant when discussing possible resistance mechanisms. Parry (1971), comparing the probing behaviour of green spruce aphid on Sitka spruce and Norway spruce, provided evidence that differences in damage symptoms between these two main host species are related to features connected with the deposition of saliva and the branching and divergence of the salivary sheath. Such differences may arise from anatomical dissimilarities probably of the parenchymatous tissue affecting stylet penetration.

Differences in host plant susceptibility do not only exist between spruce species but also on a subspecies level. In north-west European forests, the preferred host of the green spruce aphid is Sitka spruce which is in general highly susceptible to aphid attacks. Within this species conspicuous differences in the resistance to the green spruce aphid have however frequently been observed. Differences have been demonstrated both regarding natural infestation levels (Day, 1984) and regarding the response of the trees to aphid attack (Carter and Nichols, 1988). This variation is not surprising since examples of within-species variation in resistance to herbivorous pests are numerous (e.g. Hanover, 1975), and similar variation in the susceptibility of conifers to aphid attacks is to be expected. Bejer-Petersen *et al.* (1974) found that clones of *Abies alba* showed differences in susceptibility to attacks by the adelgid *Dreyfusia nordmannianae* and clonal differences in resistance in larch against *Adelges laricis* were shown by Blada (1982); several additional examples can be given.

Variation in susceptibility at provenance level

The probability of a considerable subspecies variation in herbivore resistance is particularly high in host trees with a great ecological variation. Sitka spruce is native to the Pacific fog belt along the west coast of North America, the natural range extending from Kodiak Island, Alaska to Mendocino County, California, thus spanning 22° of latitude and a distance of 1800 miles (approx. 3000 km); the longitudinal range is however quite narrow, extending only 30-130 miles (50-200 km) inland (Cannell, 1984). The genetic constitution varies considerably within its geographical range (Burley, 1966; Daubenmire, 1968; Cannell, 1984).

The expected ecotypic variation of such a species is manifest in the growth characteristics of its provenances, and it is clearly expressed when the species is introduced to the environment of European forests. Many studies of its growth in Europe have been carried out, showing a general cline for increasing vigour with decreasing latitude of seed origin (Lines, 1987). Most of the seed origins studied form part of the IUFRO (International Union of Forest Research Organizations) collections (Fletcher, 1976) from which parallel field trials have been established in several European countries and within a range of different soil and growth conditions with the primary aim of testing adaptability, quality and yield. Collection was undertaken from the entire natural range of Sitka spruce from Alaska to California. Seed was collected in stands from which commercial harvest could subsequently be undertaken, in stands where only limited harvest would be possible and in stands of scientific interest only. Some of the seed origins of the IUFRO trials appear in Figure 7.1.

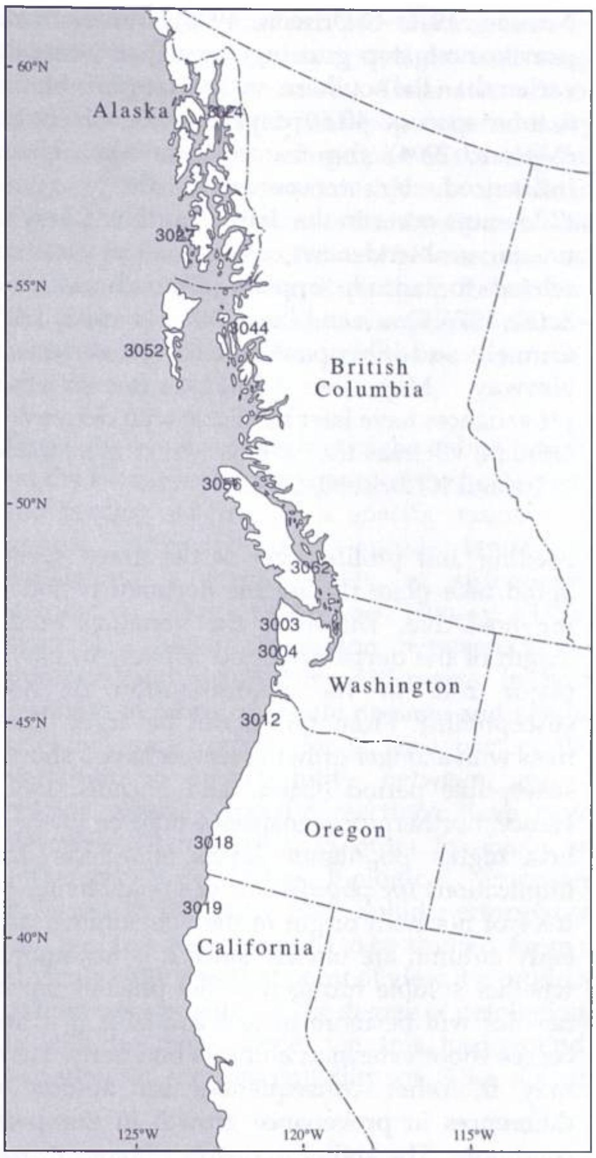

Figure 7.1 Map of IUFRO seed origins (provenances) and natural range of *Picea sitchensis*.

Much of the expressed ecotypic variation in the growth of Sitka spruce in European conditions is related to responses to photoperiod and temperature in new environments and latitudes. The major phenological difference is in the date of budset between provenances, the date of budburst remaining surprisingly similar (Lines and Mitchell, 1966). Growth cessation is strongly correlated with the original latitude of the provenance and is under strong influence of daylength (Cannell and Sheppard, 1982). At the same site northern provenances have a shorter growth period ceasing their growth and setting buds earlier in the summer than the more southerly provenances which continue growth until later in the season (Kleinschmidt and Sauer, 1976; Kraus and Lines, 1976; Magnesen, 1976;

Nanson, 1976; O'Driscoll, 1976). The northern provenances stop growing more than 2 months earlier than the southern ones. As regards budset a time span of 40-60 days has been recorded (Nielsen, 1994); this feature is to some extent influenced by temperature. Only minor differences occur in the date of budburst, and no unequivocal tendencies of systematical variation related to latitude appear (Kleinschmidt and Sauer, 1976; Kraus and Lines, 1976; Nanson, 1976; Cannell and Sheppard, 1982). However, in Norway Magnesen (1976) found that provenances have later budburst with decreasing latitude, whereas the reverse was demonstrated in Ireland (O'Driscoll, 1976).

Feeding and proliferation of the green spruce aphid take place during the dormant period of the host tree. Therefore, the variation in the length of the dormant period is likely to play a major role in the determination of host susceptibilily. From this it can be argued that trees with a longer growing season have a shorter susceptible period (Carter and Nichols, 1988). Hence, northern provenances would be likely to host higher population levels of aphids. The implications for populations of aphids living on trees of northern origin in the late summer and early autumn are unclear since it is not known whether soluble nitrogen in the phloem sap of needles will be more or less available if a tree ceases shoot extension and sets bud early. There may be other consequences for aphids of differences in provenance growth in European conditions. The ability to devote photosynthates to the production of secondary defensive chemicals in needle tissue are likely to depend on the growth of the different seed origins.

Provenances of *P. sitchensis* also differ in their responses to aphid attack. In Wales observations in a IUFRO trial showed that southerly provenances recover leader and stem incremental growth quicker after defoliation by aphids than northerly provenances which show growth depression for at least two growing seasons (Carter and Nichols, 1988). The general pattern is that the most northern provenances (typically Alaskan) have longer dormant periods, grow slower in all respects and have fewer reserves to aid recovery.

Seasonal patterns of aphid abundance on the foliage of Sitka spruce are fairly predictable (Chapter 4). In the British Isles as well as in Denmark a peak in population density is invariably reached at the end of May or the beginning of June. Samples taken throughout a forest plot on several occasions during this period showed that a reliable estimate of the peak aphid density can be obtained from a single sample at the end of May (Day and Crute, 1990). Since the peak aphid density is the most useful indicator of subsequent defoliation rate (Chapter 2), any differences in this value observed between provenances is likely to be an equally useful index of resistance/susceptibility. This reasoning formed the basis for a study of aphid populations on six provenances of Sitka spruce in a replicated IUFRO forest provenance trial in 1983 (Day, 1984). The provenances which have been studied in Northern Ireland are recorded in Table 7.1.

The main differences in aphid peak population density appear from Figure 7.2. Although a substantial proportion of the variation in aphid

Table 7.1 Sitka spruce provenances on which aphid populations have been evaluated in Northern Ireland (Day, 1984; Armour, 1996). A (Alaska), BC (British Columbia), W (Washington), O (Oregon), C (California)

Provenance Code	IUFRO Number	Origin Locality	Latitude	Longitude
A24	3024	Duck Creek	58°22′	134°35′
A27	3027	Craig	55°30′	133°08′
BC44	3044	Inverness	54°12′	130°15′
BC52	3052	Tasu Creek	52°52′	132°05′
BC56	3056	Holberg	50°37′	128°07′
BC62	3062	Big Qualicum R.	49°23′	124°37′
W03	3003	Forks	48°04′	124°18′
W04	3004	Kalaloch	47°42′	124°25′
O12	3012	Necanicum	45°49′	123°46′
O18	3018	Brookings	42°15′	124°23′
C19	3019	Big Lagoon	41°08′	124°09′

STD Standard Irish Seed Batch from Kilsheelan forest, Tipperary, Eire (included in geographical relationships as Queen Charlotte Islands latitude) numbers could be attributed to the location (block) within the experiment, more than 50% of the variation resulted from differences between provenances. This was a promising result for the potential of tree breeding for resistance, since the provenance which appeared to be the most resistant to aphids hosted only 12% of the population found on the least resistant provenance. Translated into the life of a forest, this could mean the suppression of aphid populations below a threshold level where any economic damage could be perceived (Chapters 2 and 3).

A second result of this experiment was a clear, and inverse relationship between aphid population and the original latitude of the seed origin, i.e. the southern provenances supporting the highest aphid numbers (Day, 1984). The trees at this stage were eight years old and still in the thicket stage of canopy development. A second study was carried out on the same site in 1994; two principal differences were that the trees were at 19 years old and had closed canopies for several years, and a greater range of provenances were evaluated (Armour, 1996). Differences between provenances were equally marked although there appeared to be a disparity with some of the earlier results (Day, 1984) in that the later studies (Armour, 1996) indicated a direct relationship between population density and latitude, the northern provenances being now the most infested. Laboratory experiments revealed a higher MRGR on northern provenances than on southern ones and greater weight indicating higher fecundity (see below). These two sets of data, describing aphid peak population density on provenances from a large part of the original range of Sitka spruce are considered together in Figure 7.2. However, most of the data (the middle latitudinal range) are consistent between the two studies. The only major disparity is focused on the most northerly provenance (Alaska 24) for which the aphid population in the recent survey was the highest overall.

Defoliation rate is a product of the aphid density on the foliage and the response of the host tree to the feeding activity of a specific number of aphids. Although peak aphid density is considered a useful index of subsequent defoliation (Day, 1984) and Hussey (1952) showed a linear correlation between aphid numbers and defoliation, differences in host response in terms of needle damage and needle retention may account for at least part of the variation in susceptibility between spruce origins. Species specific reactions have been described (Parry, 1971). In order to obtain an understanding of the biological processes involved in resistance both aphid performance and host tree response need to be studied. From a silviculturally practical point of view the product of both components, i.e. the degree of defoliation, is still the major issue. On this background, variation in the susceptibility of Sitka spruce

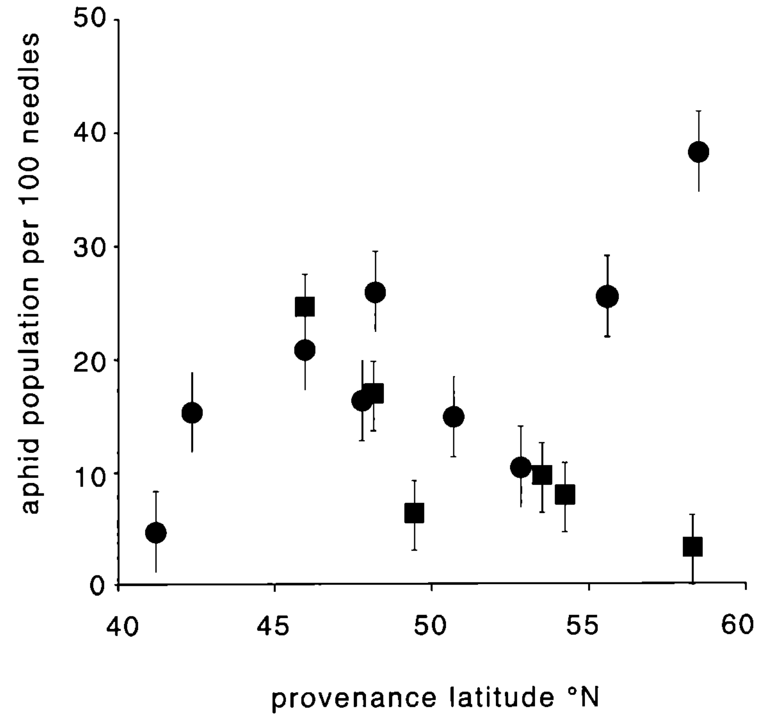

Figure 7.2 Comparative population levels of aphids at the peak density on provenances of *Picea sitchensis* originating at different latitudes in the natural range. The data represent means and standard errors from replicated plots in the same forest experiment, Springwell Forest, Northern Ireland (■ Day, 1984; ● Armour, 1996).

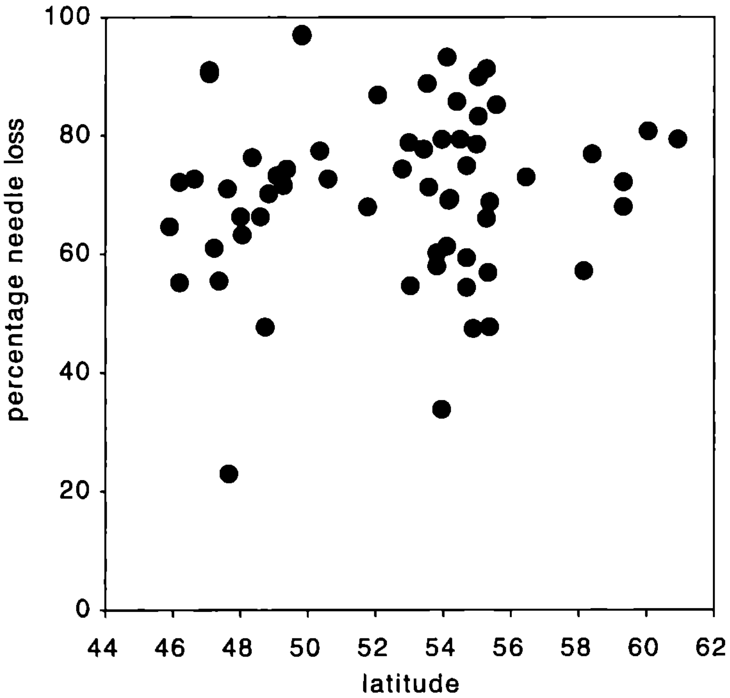

Figure 7.3 Defoliation due to aphid attack on provenances of *Picea sitchensis* originating at latitudes covering the entire natural range of the host tree. IUFRO provenance trial in Husby Plantation, Denmark.

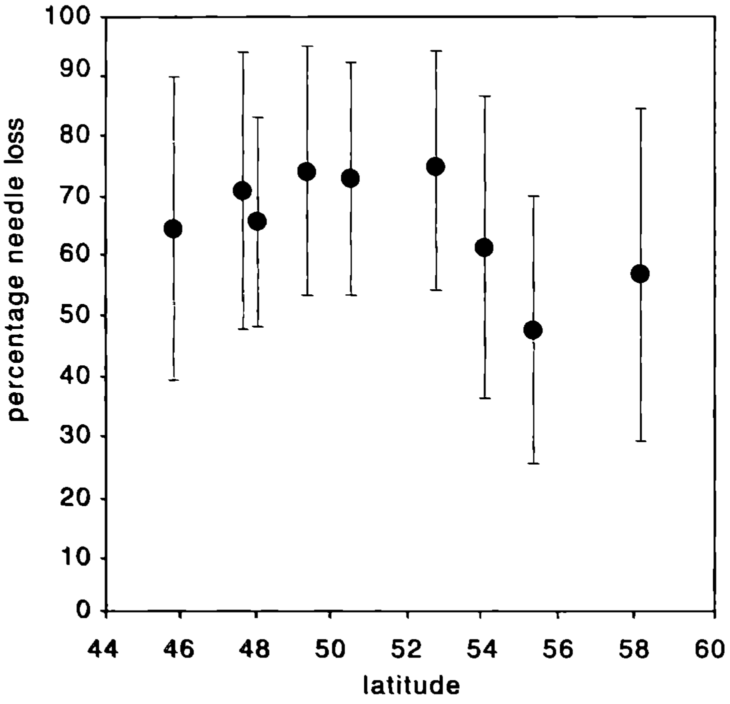

Figure 7.4 Defoliation due to aphid attack on nine provenances of *Picea sitchensis* which have been studied in Northern Ireland (Day, 1984; Armour, 1996) in terms of peak population levels. The data represent means and standard errors from plots in a IUFRO provenance trial, Husby Plantation, Denmark. (c.f.Figure 7.2)

provenances was recorded in a provenance trial in Denmark including all seed origins collected in the IUFRO provenance series (61 North American provenances plus 3 domesticated provenances), using percentage needle loss of the previous year's foliage as an index of resistance (data arc sine transformed in analysis).

Also in this forest trial a considerable variation between provenances was observed (Figure 7.3). Mean level of defoliation of the provenances varied between 23.18 and 96.85% needle loss, the average needle loss of all provenances being 71.67%. Contrary to the partly clinal trends found by Day (1984) and Armour (1996), this investigation showed no correlation between susceptibility and latitude of the seed origin (Figure 7.3). Only a very weak and statistically not significant trend could be observed, if any at all, of slightly increasing defoliation with increasing latitude (Harding, unpublished). In Figure 7.4 the percent needle loss of the provenances studied in the Northern Irish investigations by Day (1984) and Armour (1996)

(Figure 7.2) are shown for comparison. No support is given to the hypothesis of an influence of latitude on resistance.

As indicated by the standard errors shown in Figure 7.4, one important finding in the Danish studies is a substantial variation in resistance between individuals within the same provenance. Almost all provenances included individual trees with 100% defoliation of the one-year-old needles as well as totally undefoliated trees. From this it is evident that tree characteristics related to provenance alone cannot be the only factor determining host susceptibility, a finding which gives good prospects for resistance breeding (see below).

There was an interesting trend in the results of Day (1984) and Armour (1996) in which aphid population density was highest on provenances which are slower growing (Lines, 1987). In particular, the British Columbian provenances which are well-adapted to the maritime British climate and which perhaps retain genes from preglacial populations in glacial refuges (Warner *et al.*, 1982; Lines, 1987) were among the least populated by the green spruce aphid (Figure 7.2). This higher degree of adaptation results in decreased stress inflicted on the host tree (Armour, 1996). The same trend was not observed in Denmark, where Washington, British Columbia and Queen Charlotte Islands provenances did not deviate from less adapted seed sources. With the exception of one, which has been particularly selected for putative aphid resistance (see below), the domesticated provenances were not less attacked by the green spruce aphid.

In the Danish investigation, damage from aphid infestation appeared to be related to tree height. Visually, the trial gave the impression that the most vigorously growing trees were the most heavily damaged. This was not expected from the results by Day (1984) and Armour (1996) that lower densities were attained by the best-adapted origins. However, statistical analysis clearly demonstrated a strongly positive correlation between the height of the tree and proportion of needles lost (Linear regression, $F = 21.25$, $df = 509.2$, $P < 0.0001$) (Harding, unpublished), indicating that growth-related features play a major role in the development of damage.

A profound effect of height on defoliation level was also evidenced by observations in Iceland (Halldórsson, unpublished). A plot with seven Sitka spruce provenances in Jórvík in eastern Iceland was attacked for the first time by the green spruce aphid in the autumn 1991. The provenances all originate from the western coast of Alaska (Table 7.2) and the trees had been planted as 4-year-old saplings in 1973.

Damage due to the green spruce aphid was estimated in the spring of 1992 using percentage needle loss plus percentage damaged needles as an index of damage. From the assessment it was obvious that damage was positively correlated with the height of trees. As regards the relationship between susceptibility and latitude, the Icelandic results indicate that the northernmost Alaskan provenances are the most suitable hosts for the green spruce aphid. Damage was weakest on the provenance from Afognak Lake. Damage on the remaining provenances was of a similar level, but the southernmost provenance, Miller Point, was second lowest in damage rank (Figure 7.5). No significant trend in the relationship between damage and original latitudinal origin of seed could however be found (Halldórsson, unpublished). Therefore, the populations of aphids or their effects on trees can be shown to vary substantially with provenance, and even systematically with origin latitude, but neither effect is necessarily temporally or spatially stable. Provenance differences at the same site may reverse, although this may be a result of changes in crop development as canopy closed from 8 to 19 years after planting. In addition, assessments in different countries do not always reveal the same result for a similar provenance range.

What dictates the differences observed in peak population density of aphids among the range of Sitka spruce provenances studied ? The estimates of peak population (Armour, 1996) were accompanied by population samples at regular intervals throughout most of the year on the same provenance range. The most striking differences in population growth rate were observed in the late spring and early summer, prior to budburst. To index the growth rate, lines were drawn through linear increases in population density over time up until the population on each provenance reached a maximum. The slope of each line provided the index (Figure 7.6) and was considered to be an adequate descriptor in field conditions with variable temperature, even though, in many years, population growth in this phase appears to be exponential (Chapter 4). Peak population density for each provenance was strongly related

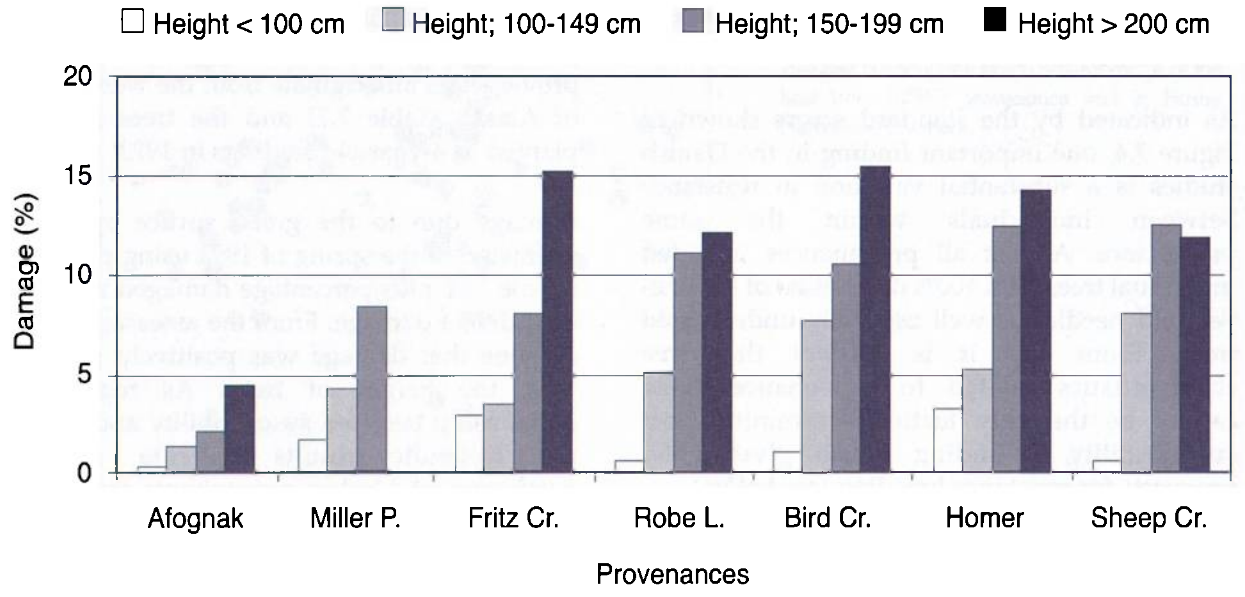

Figure 7.5 Damage by the green spruce aphid on seven provenances of *Picea sitchensis*, Jórvík, Iceland.

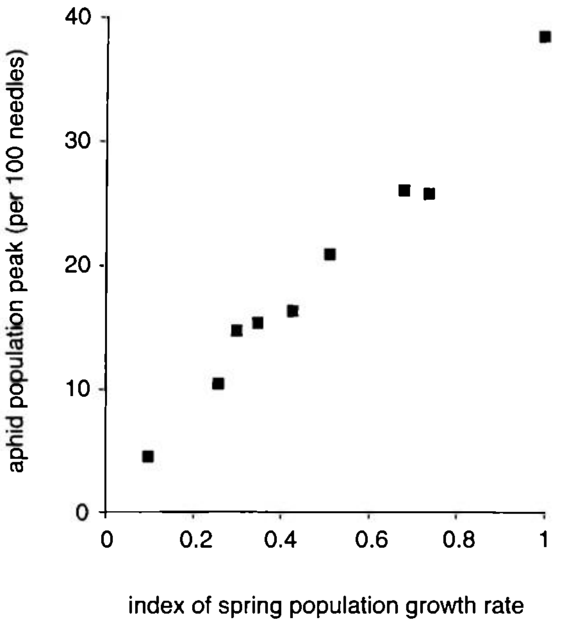

Figure 7.6 The relationship between peak aphid population reached on each provenance and the index of population growth (see text) derived from field populations in May (Armour, 1996).

Table 7.2. Sitka spruce provenances on which aphid attack has been assessed as percentage needle loss, Jórvík, Iceland

Origin of provenance	Latitude	Longitude
Sheep Creek, Lowe River, Valdez	61°07′	145°48′
Robe Lake, Valdez	61°05′	146°05′
Bird Creek, Turnaigin	60°58′	149°26′
Fritz Creek, Chinitna Bay	59°48′	153°11′
Homer Hills, Kenai Peninsula	59°40′	151°30′
Afognak Lake, Afognak Island	58°05′	152°59′
Miller Point, Kodiak Island	57°50′	152°22′

to the growth index (Figure 7.6) and emphasised the importance of the response of aphids to trees during May.

Mean relative growth rate of aphids (MRGR), measured on plant material in laboratory conditions, is a good indicator of their population rate of increase (r_c) (Dixon, 1985) and can measure differences in performance at various times during the growing season. This approach was adopted for the provenance experiment because population density in the field was often too low for census to be carried out, yet dynamic change even at low density is equally significant to the peak population in future (Chapter 4). It was necessary to measure MRGR on excised shoots because whole trees of suitable dimensions were not available for growth chamber work (Armour, 1996), but as a result it is possible that all replicates performed below field potential since most MRGR's were below maximum expectations (MRGR >0.3 for $r_c = 0.25$, Dixon, 1985) (Figure 7.7). Nevertheless, two periods (April and November, when sap nutrient levels are highest) provided the most significant differences in aphid MRGR between provenances.

Fertility rates of aphids individually reared on excised shoots from a range of provenances in the field experiment, confirmed these differences in population growth rate and performance. Fertility was assessed in July, October and March and in only the latter month were significant differences associated with provenances (Figure 7.8). The Alaskan provenance (A24) hosted

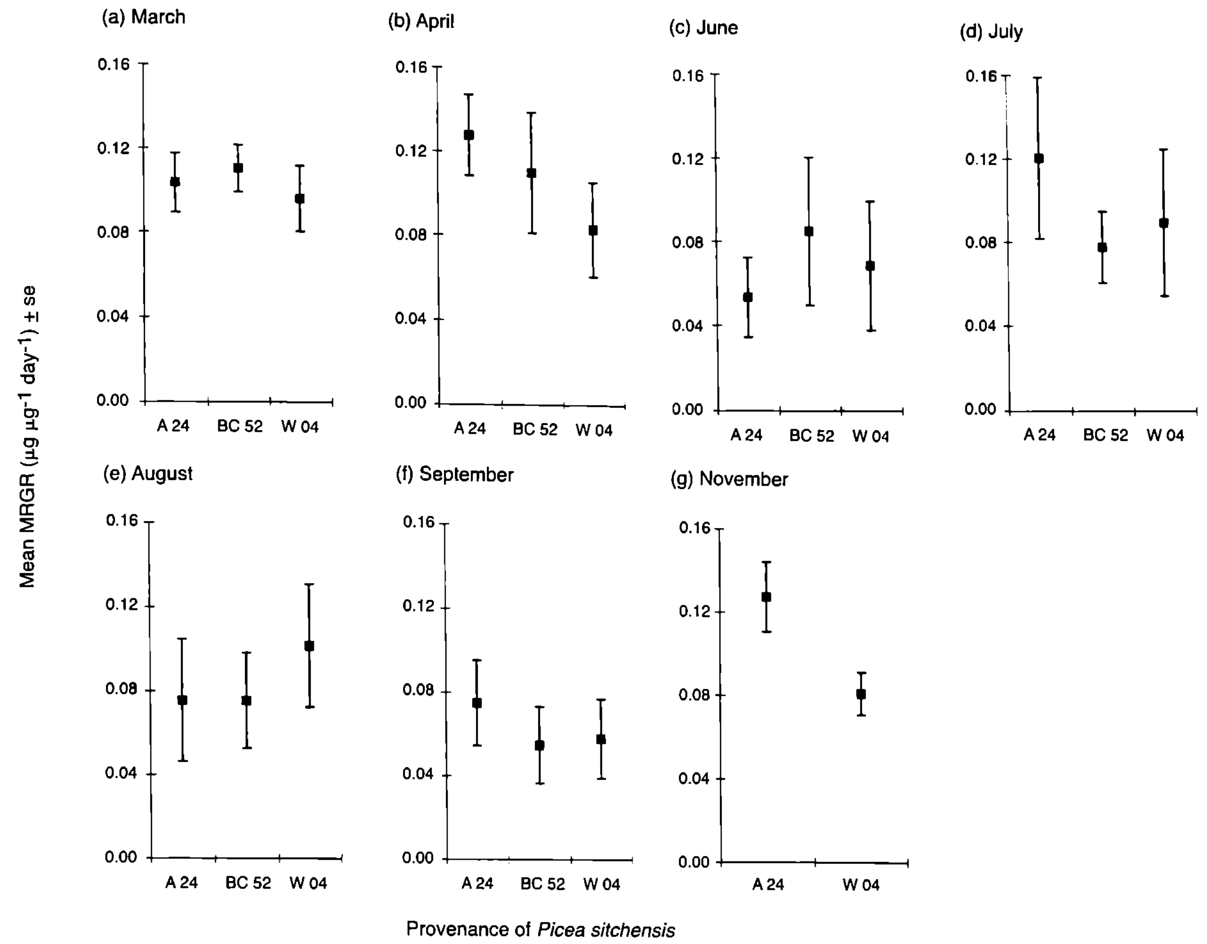

Figure 7.7 Mean relative growth rates (MRGR) of aphids on replicated, excised shoots of three provenances (A24, BC52 and W04) in growth chambers at 14°C. There were significant differences in MRGR ($P<0.05$) between provenances in April and November (Armour, 1996).

aphids with significantly higher birth weights and a higher mean lifetime fertility in March (Armour, 1996).

Finally, account was taken of the progress of aphid populations on three selected provenances over winter. The winter of 1994/5 was relatively mild, even for Northern Ireland (Day and Crute, 1990), temperature never reached -5°C and there were no sudden temperature changes and limited chill periods. Consequently aphid populations were not expected to decline dramatically through high mortality, and it was not expected that differences in survival on the different provenances would be due to differences in needle supercooling point (Powell and Parry, 1976). Natural populations were monitored from 13 December 1994 and throughout the winter on marked shoots, and changes documented as a percentage of the initial population density (Figure 7.9). Population showed a marginal increase on the Alaskan provenance (A24) whereas the other populations (O12 and W04) declined progressively.

The major differences in population dynamics of aphids on trees of different provenance are most clearly detected during periods in the tree growth season when the performance and population growth rate are strongest. The most significant periods are May and possibly November, although the ability of aphids to take advantage at this time of year depends on ambient temperature. Mild winters magnify differences in aphid potential on different provenances. The functional relationships between aphids and provenances could be reliant on either sap nutrients or secondary chemistry, at present neither can be ruled out. The first hypothesis is that the reponse of aphids to trees from the most susceptible provenances is a product of a greater availability of sap nutrients at critical times. Greater nutrient availability would be expected in faster growing trees, generally from the more southerly provenances (although the latitudinal cline is by no means linear in this respect, see Lines, 1987). This is not supported by the data from Northern Ireland which suggest that faster growing provenances are more resistant.

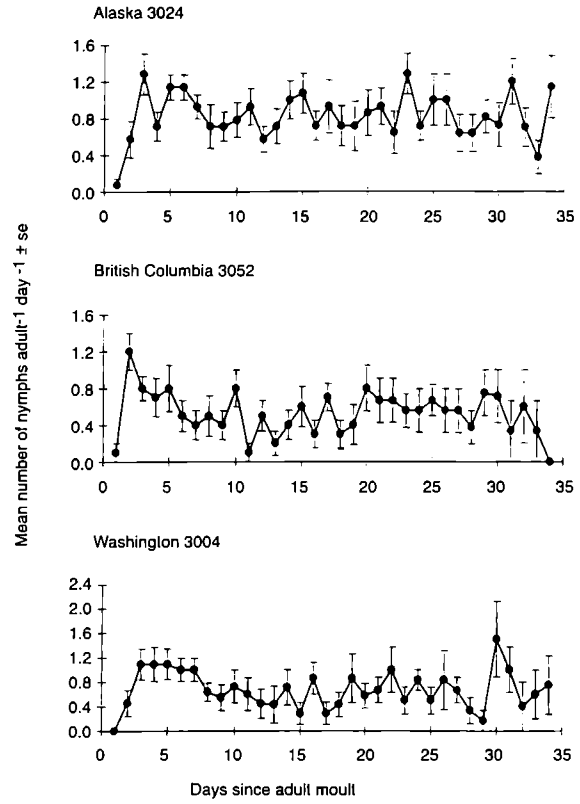

Figure 7.8 Fertility patterns of replicated individual adult apterous aphids on each of three provenances (A24, BC52 and W04) (Armour, 1996).

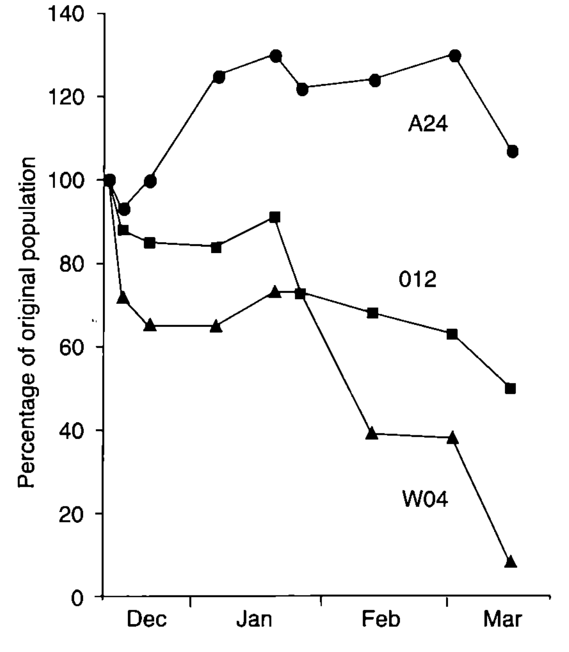

Figure 7.9 The relative survival and growth of replicated natural colonies of aphids on trees of three provenances throughout winter 1994/5 (Armour, 1996).

A second hypothesis suggests that secondary defensive chemicals, perhaps in the form of volatile epicuticular compounds (*sensu* Jackson and Dixon, 1996), form a greater investment in faster growing trees and it is this difference between provenances which represents the basis of resistance. Finally, structural characteristics such as needle anatomy could turn out to be important barriers to aphid access to the plant, but so far this has not been a subject of investigation.

Variation in susceptibility at family level

Within forest stands of Sitka spruce individual variation in the relative abundance of aphids and in defoliation due to the green spruce aphid is regularly observed, strongly indicative of a differential susceptibility at a sub-provenance level. Likewise, substantial intra-provenance variation in aphid density was demonstrated in the IUFRO provenance studies by Day (1984). Similar obvious differences in the degree of defoliation within provenances were recorded in the IUFRO trial examined in Denmark (Harding, unpublished). Here, variation from 0 to 100% loss of the previous year's needles could be found within the same provenance even between neighbouring trees of the same height with intertwining branches, ensuring that no physical barriers limited the dispersal of aphids.

It is unquestionable that characteristics unrelated to provenance are also contributory to the determination of susceptibility. Until now, investigations of host tree resistance to the green spruce aphid have dealt exclusively with differences between tree species and provenances, trying to explain the variation by phenology-mediated differences in nutritional sap constituents or by secondary substances, but recent research has shown that significant variation in the resistance of Sitka spruce to the green spruce aphid exists also at a family level (Jensen *et al.*, 1997).

Variation between families of Sitka spruce was investigated in a progeny trial in Denmark with 14 open pollinated progenies from a clonal seed orchard established from scions harvested from putatively resistant trees (Jensen *et al.*, 1997). Following a heavy attack by the green spruce aphid in 1957 (Bejer-Petersen, 1957) a 51-year-old stand of Washington origin was fatally damaged leaving only 50 surviving trees. A clonal seed orchard was established from the most vital trees and although never tested, plants originating from the seed orchard (Vosnaes) have been designated 'aphid resistant' (Anon., 1991). Three progeny trials were established in 1972 in which the progenies are being tested along with a reference provenance (Frijsenborg, Washington origin) plus a commercial seedlot from the seed orchard (Jensen *et al.*, 1996).

In 1989 a major outbreak of the green spruce aphid occurred in Denmark (Bejer and Harding, 1990) and one of the progeny trials located in a typical 'aphid area' close to the North Sea was seriously attacked. This attack offered an excellent opportunity to make the first systematic investigation of variation in resistance at family level. In addition, analyses of the correlation between growth parameters and aphid resistance could be made as measurements of height, diameter and pilodyne (estimate of wood density) had been carried out in 1986 (Jensen *et al.*, 1996). It was not possible to make comparative studies of aphid population density and subsequent defoliation and susceptibility was therefore evaluated in terms of damage of the individual trees. In February 1990 percentage needle loss of the previous year's foliage was assessed with the aim of studying the consistancy of resistance. The assessment was repeated in February 1992 following a minor attack in early summer 1991.

Although relatively large environmental effects in relation to family effects occurred, statistically significant differences between families in 1990 were demonstrated ($F = 3.62$, $P < 0.001$). The mean percentage of needle loss varied between 3.9% for the best family to 22.3% in the most heavily defoliated family (Table 7.3). The family that appeared to be most resistant suffered a needle loss which was only about 10% of that of the standard provenance.

The second important finding of this investigation was that resistance is inherited by the offspring and can be demonstrated many years after selection for the trait. The seed orchard was established by vegetative propagation from undefoliated trees about 30 years before the assessment of the needle loss of the offspring, yet all families were significantly ($P < 0.0001$) less defoliated than the domesticated reference provenance, which had an average level of defoliation of 37.4 %.

This significant superiority of the Danish seed orchard in Vosnaes to other Sitka spruce provenances, even of Washington origin, regarding the level of aphid resistance appears to be a general and consistent character which has been observed in several provenance trials. Vosnaes was the second least defoliated provenance in the Danish IUFRO trial (Harding, unpublished), exhibiting a degree of defoliation less than 45% of the most severely damaged provenance. In Norway a comparison of Sitka spruce seed origins showed a significantly higher level of resistance to the green spruce aphid in the Vosnaes material (Saeby and Taksdal, 1994).

No significant differences between families could be shown following the minor attack in 1991, indicating that the degree of attack plays an important role in pinpointing differences in resistance. Despite the moderate level of defoliation all selected families were found to be significantly less affected by needle loss than the reference provenance, clearly demonstrating the prospects for selection for aphid resistance.

The family heritability was calculated as 0.72. The standard deviation for needle loss was very high - a circumstance which along with the high family heritability leads to an expectation of high gains from selection for this trait. Assuming perfect normality and a selection of three families with least needle loss out of the 14 families tested, giving a selection intensity of 1.271 (Becker, 1974), an actual response of 54% and a relative response of 37% improvement on aphid resistance based on needle loss could be estimated (Jensen *et al.*, 1997). Such high responses are seldom observed, and give very promising prospects for including aphid resistance as an important parameter in breeding programmes. In comparison, the relative response to a similar selection based on height - a trait normally included in tree improvement programmes - was 16% improvement.

Possible correlations between aphid resistance and growth parameters are of major importance in relation to the advantages of including aphid resistance in future tree improvement programmes. Phenotypic correlations between needle loss, height, diameter and wood density were calculated in the progeny trial and apparently no significant correlations exist between these characters. However, a negative correlation between wood density and needle loss may be present in this investigation (Jensen *et al.*, 1997).

The results of the genetic variation appearing in the investigations of resistance at family level offer no additional specific information about the biological mechanisms and processes

Table 7.3 Average needle loss in 1990 and in 1992 due to attacks by the green spruce aphid in a progeny trial consisting of 14 families from a clonal seed orchard of selected putative aphid resistant trees, a commercial seed lot of the seed orchard and a reference provenance (Data from Jensen *et al.*, 1997)

Family	Needle loss 1990, %	Needle loss 1992, %
8052	18.0	13.3
8053	17.2	12.0
8054	20.3	9.8
8055	22.3	9.4
8056	11.6	11.8
8057	17.8	12.3
8058	18.2	7.8
8059	3.9	5.7
8060	17.4	14.0
8061	9.8	10.7
8062	15.3	12.1
8064	16.4	10.3
8065	7.2	5.2
8066	9.4	4.3
Mean of families	14.6	10.1
Commercial seed lot	14.0	9.8
Reference provenance	37.4	21.1

determining host tree susceptibility to the green spruce aphid. An increased understanding which may aid in the future search for the underlying processes is however given by the important knowledge that resistance is inherited and the indication that the trait appears to be relatively consistent in time and space.

Variation in susceptibility at clonal level

In their investigations of family resistance to the green spruce aphid Jensen *et al.*, (1997) found a substantial variation within families. In several families some individuals were absolutely unaffected by aphid attack whereas others showed a high percentage of needle loss, suggesting that differential susceptibility is likely to be found also at a clonal level. This is also indicated by Armour (1996) in field observations of natural abundance of the green spruce aphid.

Resistance at clonal level has so far not been thoroughly studied. However, preliminary observations have been made in connection with the attack by the green spruce aphid in Denmark 1989 (Harding and Roulund, unpublished). Nineteen clonal trials all established in 1986 were inspected for aphid attacks, of which nine were recorded for differences in susceptibility to the green spruce aphid. Aphid damage was evaluated by visual assessment of needle loss, using a percentage scale for the whole tree. Seven of these nine trials were however too weakly defoliated for further analysis, but the remaining two trials were severely defoliated. In these two clonal trials - one located in the island Roemoe, the other in eastern Jutland (Frijsenborg) - 151 clones of domesticated Sitka spruce (Roenhede F.405, presumably of Queen Charlotte Islands origin) were tested.

The evaluation of needle loss showed significant differences between clones in both trials ($P < 0.001$). The attack was heavier at Roemoe, where mean percentage needle loss varied between 0 and 42.5, at Frijsenborg the mean level of defoliation for the clones varied between 0 and 34.9%. A second observation series was undertaken in 1992 following a moderate aphid attack, and again both trials showed statistically significant differences between clones ($P < 0.0001$). The ranking of clones was surprisingly identical in the two records, indicating a high degree of consistancy in the expression of resistance. Consistancy of resistance in time and space is again an issue of great practical importance which awaits further research.

Selection for resistance and the prospects for practical use

The great variation in susceptibility to the green spruce aphid exhibited by different provenances, families and clones of Sitka spruce which has been demonstrated in forest stands and field trials provides promising prospects for including aphid resistance as an important trait in future tree improvement programmes of Sitka spruce.

Optimization of timber production is the ultimate aim of the programmes, hence selection of the best adapted seed origins as regards survival, vigour and yield is invariably given the highest priority. Yet, growth losses due to aphid attacks may be substantial (Chapter 2) and use of plant material with a high degree of resistance would undoubtedly improve productivity.

The choice of seed origins of Sitka spruce for north-west European forestry is closely connected to the climatic conditions within the specific region, especially to the risk of frost during late spring and early autumn. Frost thus sets the most influential limitations on the range of provenances that can be used. The latitude of the original seed - and through this the likeliness of frost damage - may influence the susceptibility of the provenances to aphids (Day, 1984; Armour, 1996; Halldórsson, unpublished), although clinal trends are not certain and no influence has been found in other trials. The best climatically adapted provenances may however not be the most suitable with respect to aphid damage. In Iceland, the Alaskan provenances are the only option since the threat of frost strongly influences tree survival. These northern provenances appear to be less resistant to aphids than southern provenances which cannot grow in the Icelandic climate. Conversely, the 'aphid resistant' Danish provenance Vosnaes is unsuitable in localities prone to spring frost and is for this reason not widely used.

An important result from the investigations on resistance to the green aphid is that the choice of provenance appears not to be crucial for developing aphid resistance among breeding stock. Within-provenance variation has been demonstrated to be great, ranging from apparently absolute resistance to such a high degree of susceptibility that total defoliation can be expected during major attacks. Probably within all provenances, families or individuals can be found with a very high degree of resistance, which can constitute the source of plant material for tree improvement. Secondly, there appears to be no negative interactions between resistance and the growth parameters on which current breeding programmes are based, i.e. selection for aphid resistance should be possible without having to dispense with the requirements of quality and yield.

Furthermore, resistance is inherited by the offspring and - as far as this issue has been studied - the character appears to be more or less consistent in time and perhaps also in space. High gains can be expected by selection from the substantial family heritability and the great variation within families. In general, with strong selection for height growth on the basis of family and clone testing, a gain of 15-20% can be predicted in relation to average Danish provenances (Nielsen, 1994). Given a similar selection for aphid resistance even higher gains can be predicted (Jensen *et al.*, 1997).

In conclusion, the advantages of including resistance to the green spruce aphid in current tree breeding programmes are obvious and on the basis of present knowledge the prospects for success appear to be very positive. A basic understanding of the mechanism of host tree resistance to the green spruce aphid would give tree breeders a considerable advantage, perhaps allowing the development of screening methods.

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Chapter 8

Atmospheric pollution, elevated CO_2 and spruce aphids

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Summary

The effects of atmospheric pollutants on agricultural and forest pests have been studied extensively in the last 10 years. This research has included work on several tree-dwelling aphid species, such as *Elatobium abietinum* and *Cinara pilicornis* on *Picea sitchensis,* and *Cinara pini* and *Schizolachnus pineti* on *Pinus sylvestris.* These studies have shown that exposure to SO_2 and NO_2 consistently enhances aphid performance (as typically measured by relative growth rate). Work on ozone has produced less consistent results.

The effects of atmospheric CO_2 have been studied on a range of tree-dwelling insects including. *E abietinum, C. pilicornis, C. pini, Phyllaphis fagi* on *Fagus sylvatica,* and *Drepanosiphum platanoidis* on *Acer pseudoplatanus.* Published research on plant-chewing insects has shown that elevated CO_2 tends to have a detrimental effect on insect performance. Research on aphids, however, has produced less consistent results, although spruce aphids appear to perform less well on plants exposed to elevated rather than ambient CO_2.

It is concluded that future research effort on atmospheric pollutants and elevated CO_2 should (a) concentrate more on aphid pests (b) study the combined effects of factors such as CO_2, drought, temperature, plant nutrient status, and pollutants such as ozone, and (c) focus on the consequences of the results obtained for the abundance and damage caused by forest pests.

Introduction

It has long been suspected that atmospheric pollution plays a significant role in stimulating the outbreaks of insect pests. Beling (in Escherich 1931), for example, reports on an outbreak of *Epinotia tedella* (Clerck) in 1831 in a smoke damaged young spruce stand in the Harz mountains. In recent years, circumstantial evidence for the effect of atmospheric pollution on insect pests has been augmented by experiments on a wide range of insect herbivores, including several agricultural and forest pests (McNeill and Whittaker, 1990; Whittaker, 1994; Brown, 1995; Docherty *et al.,* 1997a). These pests have included several aphid species such as *Elatobium abietinum* and *Cinara pilicornis* on *Picea sitchensis,* and *Cinara pini* and *Schizolachnus pineti* on *Pinus sylvestris.* This chapter summarises research on these species.

In contrast to the concerns about the effects of atmospheric pollution on insect pests, there has been very little interest in the effects of climate change until recently. This is not to say that the impact of most aspects of climate change have not been extensively studied: much has been written about the effects of temperature, in particular, on insects (e.g Uvarov, 1931; Andrewartha and Birch, 1954; Lawton 1995). However, the growing realisation that the increase in concentrations of greenhouse gases is leading to global warming (Houghton *et al.,* 1992; Bennetts, 1995) has given an extra significance to previous research on the effects of temperature on insects as well as sending this research in new directions (Dewar and Watt, 1992; Harrington, Bale and Tatchell, 1995; Sutherst, Maywald and Skarratt, 1995).

The rising concentration of atmospheric CO_2 has also led to research on the effects of elevated atmospheric CO_2, mainly on plants (Eamus and Jarvis, 1989; Bazzaz, 1990; Dahlman, 1993) but also on insect herbivores (Watt *et al.* 1995; Docherty *et al.* 1997a). Although the effects of atmospheric CO_2 on many insect herbivores has been studied, until recently, no work had been done on forest pests and the emphasis of the research had been on plant-chewing insects. However, recently completed research projects at Lancaster University and ITE Edinburgh have focussed on a range of tree-dwelling insects including *Elatobium abietinum, Cinara pilicornis, Cinara pinea, Phyllaphis fagi* and *Drepanosiphum platanoidis*. This chapter discusses published and unpublished research on these and other species.

Aphids and atmospheric pollution

Studies on the impact of atmospheric pollutants on insects

Circumstantial evidence on the impacts of pollutants on forest and other pests has been accumulating since the mid-19th century (Brown, 1995). In recent years, a number of outbreaks of insects have been attributed to the effect of air pollution (e.g. Wentzel and Ohnesorge, 1961; Templin, 1962; Sierpinski, 1966; Flückiger *et al.*, 1978; Przybylski, 1979). Recent examples include reports that aphids on *Pinus sylvestris* are affected by industrial pollutants, some species being more abundant near the sources of pollution, some less abundant (Villemant, 1981; Heliövaara and Väisänen, 1989). In addition, a survey of the abundance of aphids in the UK, using data collected by the Rothamsted Insect Survey, showed that the abundance of 39 aphid species was positively correlated with SO_2 concentrations, 34 species were uncorrelated with SO_2 concentrations, and only one species was negatively correlated with SO_2 concentrations (Houlden, McNeill and Bell unpublished, in Brown, 1995).

Such evidence suggests that atmospheric pollution may be having a significant impact on the status of forest and agricultural pests, but it does not clearly establish the link between atmospheric pollution and insect abundance, nor demonstrate the causal connection between the two. In particular, it is unclear from these observations whether atmospheric pollution is affecting insect pests directly, indirectly through their host plants, or indirectly through the natural enemies of insect pests.

Aphids, SO_2 and NO_2 pollution

Experiments along pollution gradients have gone some way in establishing the role of atmospheric pollutants. For example Holopainen *et al.* (1993) studied the effect of SO_2 concentrations by placing *Pinus sylvestris* and *Picea abies* saplings 0.2 to 4.5 km from a SO_2 emitting pulp mill and infesting them with *Schizolachnus pineti* and *Cinara pilicornis*. The abundance of the former aphid species was not affected by distance from the pollution source, but *Cinara pilicornis* reproduced fastest near the source. Similar investigations have been done by Braun and Flückiger (1984) near a motorway with high NO_x pollution where *Crataegus* sp. was heavily infested with *Aphis pomi*. In that study, potted *Crataegus* plants were exposed at different distances to the motorway and infested with *Aphis pomi* in open and closed cages to study the effect of parasitoids and predators such as Coccinellidae, Syrphidae and Cecidomyidae. Close to the pollution source the development of the aphid population increased significantly but the number of natural enemies was only 8.7 per 10 000 aphids compared to 21.3 at the control site 200 m from the source of the pollution.

Experiments carried out in closed or open-top chambers have provided the best evidence for the effect of pollutants on host plant-insect pest relationships. Dohmen *et al.* (1984) describe an increased growth rate of *Aphis fabae* feeding on *Vicia faba* previously fumigated with 400μg m^{-3} SO_2 or NO_2. Direct fumigation of aphids on artificial diets with SO_2 or NO_2 had no effect. Houlden *et al.* (1990) measured the relative growth rate (RGR) of eight aphid species on six agricultural crops. Fumigation with SO_2 or NO_2 led on average to an increase in relative growth rate of 19% (12 cases) and 26% (9 cases). The effect of fumigation was found to be concentration dependent. SO_2 fumigation up to 100 nl l^{-1} led to an increase in the RGR of *Acyrthosiphon pisum* on peas, above this concentration to a decrease in RGR (Warrington, 1987).

The impact of SO_2 and NO_2 on the conifer aphids *Elatobium abietinum, Schizolachnus pineti* and *Cinara pilicornis* has also been studied in closed chamber experiments. Exposure to SO_2 led to an increase in the relative growth rate and abundance of *Elatobium abietinum* on Sitka spruce (McNeill *et al.*, 1987; Warrington and Whittaker, 1990). Exposure to NO_2 has also been found to increase the relative growth rate of *Elatobium abietinum, Schizolachnus pineti* and *Cinara pilicornis* (Brown *et al*, 1993). In chamber experiments with filtered and non-filtered air along a motorway with NO_2 concentrations up to 1500 μg m^{-3} the population development of *Aphis pomi* on *Crataegus* sp. and of *Aphis fabae* on *Viburnum opulus* was significantly greater in the non-filtered chambers (Braun and Flückiger, 1985; Bolsinger and Flückiger, 1984). However, there is some evidence that biochemical changes of the host plants due to pollution effects are responsible for the changed aphid growth. Plants in the non-filtered conditions showed significantly increased contents of soluble nitrogen as amino acids and amides in the phloem sap. Experiments with artificial diets have shown that increased concentrations of amino acids have a positive effect on aphid performance (Bolsinger and Flückiger, 1989). Kidd (1990), however, could show positive or negative associations between amino acids and phenolics in the phloem sap and the growth values of *Cinara pini*. They suggest that the overall concentrations of amino nitrogen may be less important to aphid performance than the number and relative amounts of individual amino acids.

Aphids and impact of ozone

The effect of ozone on aphid performance is still poorly understood. Studies have demonstrated a positive impact in seven cases, a negative impact in four cases and no effect in seven cases (Heliövaara and Väisänen, 1993; Holopainen, *et al.*, 1994). Only one conifer aphid has shown a positive response to ozone exposure, *Cinara pilicornis* on Sitka spruce (Brown *et al.*, 1993) and on Norway spruce (Holopainen *et al.*, 1994). Exposure to ozone had no significant effect on *Elatobium abietinum* and no effect or a negative effect on *Schizolachnus pineti* (McNeill and Whittaker, 1990). The same ozone treatment can produce different biochemical responses in different food plants. In a fumigation experiment with non-filtered, ambient ozone concentrations and filtered air conditions, the growth rate of a population of *Aphis fabae* on *Phaseolus vulgaris* was significantly decreased whereas the population growth rate of *Phyllaphis fagi* on *Fagus sylvatica* was significantly increased under the same conditions. *Fagus* showed, in contrast to *Phaseolus*, a significantly increased amino acid concentration in the phloem sap in the ambient, ozone rich condition (Braun and Flückiger, 1989). It is suggested that food plant quality, influenced by ozone, might be of predominant importance for aphid performance.

Aphids and acid deposition

Acid deposition such as NH_4^+, NH_3, HNO_3, H_2SO_4 and HCl may lead to acidification of the leaf surface (Hoffman *et al.*, 1980). Klingauf (1982) showed that *Acyrthosiphon pisum* has a preference for slightly acid (plant surface) in comparison to slightly alkaline (phloem sap) conditions. Hence, acid deposition on plant surface might lead to an increase in aphid settling. Individual and population growth of *Schizolachnus pineti* was promoted by treatments of its host plant *Pinus sylvestris* with acid mist (Kidd and Thomas, 1988). Kidd (1990) showed that the growth rates of *Schizolachnus pineti, Eulacnus agilis* and *Cinara pini* on *Pinus sylvestris* were increased by 12, 20 and 100% respectively. On the other hand, the growth rates of *Phyllaphis fagi* on beech and of *Aphis fabae* on *Phaseolus* were inhibited when host plants were treated with acid mist (Braun and Flückiger, 1989).

However, the generally increased N deposition since the 1950s may also increase aphid performance in natural and semi-natural ecosystems like forests. Studies in Switzerland revealed that the average N deposition to forests between 1900 and 1950 was about 11 to 13 kg N ha^{-1} a^{-1} and more than 30 kg N ha^{-1} a^{-1} between the 1960s and the 1990s. N supply of beech increased from 1984 to 1995 by 15%. Experiments with *Phyllaphis fagi* show that with increasing N supply of beech individual and population growth of aphids increase significantly (Flückiger *et al.*, 1997). Hence it is suggested that the changing nutritional status of forest trees will affect the performance of pests.

Aphids and atmospheric CO_2

Trends and sources of atmospheric CO_2

CO_2 is the most important of the 'greenhouse' gases (excluding water vapour) responsible for global warming through the absorption and re-emission of infrared radiation in the atmosphere (UK CCIRG, 1996). CO_2 and the other greenhouse gases, water vapour, ozone, methane and nitrous oxide and clouds keep global temperatures at about 33°C higher than they would otherwise be. However, the concentration of CO_2 in the atmosphere has risen from a pre-industrial level of about 280 μmol mol^{-1} to its current level of about 355 μmol mol^{-1}, and rose at around 1.8 μmol mol^{-1} per annum during the 1980s (Houghton *et al.*, 1992). The rise in atmospheric CO_2 levels slowed during the early 1990s but has recently started to increase (UK CCIRG, 1996). It is estimated that atmospheric CO_2 will reach 600 μmol mol^{-1} before 2075, and be double the current level in about 100 years (Houghton *et al.*, 1992).

The rise in atmospheric CO_2 is due to fossil fuel consumption and cement production (5.5 ± 0.5 GtC/yr, 1980-89) and land-use change (1.6 ± 1.0 GtC/yr) (UK CCIRG, 1996). Most of the effect of land-use change is due to tropical deforestation, but this is partly balanced by carbon sequestration due to reforestation in the Northern Hemisphere at mid and high latitudes which is thought to be responsible for a net sink of 0.5 ± 0.5 GtC/yr, leading to a revised estimate of 1.1 ± 1.2 GtC/yr (UK CCIRG, 1996). Thus the consumption of fossil fuels is clearly the major source of atmospheric CO_2.

The increase in atmospheric CO_2 is thought to lead to an increase in crop productivity as a result of enhanced photosynthesis, reduced photorespiration and increased water use efficiency of plants in elevated atmospheric CO_2 (Bazzaz, 1990). However, when the availability of water and nutrients is taken into account the 'CO_2 fertilisation' effect, estimated to increase photosynthesis by 20-40%, is likely to be reduced by about half (UK CCIRG, 1996). Although plant productivity may rise under elevated CO_2, increasing the size of the resource for insect pests, evidence from studies on the biochemical changes in plant foliage under elevated CO_2 suggests that the quality of the resource is poorer under elevated CO_2 due to an decrease in the concentration of foliar nitrogen and an increase in carbon-based allelochemicals (Watt *et al.*, 1995).

Studies on the impact of elevated CO_2 on insects

Published studies on the impact of elevated CO_2 on insects on trees are limited to six leaf-chewing insects on eight trees, a total of 14 insect-plant interactions (Table 8.1). Recently completed, but as yet unpublished, studies on other leaf-chewing and leaf-mining insects takes these totals to nine insect species on eleven trees, a total of 19 insect-plant interactions (Table 8.1). In addition, experiments have been carried out on eight plant-sucking insects on five tree species, a total of eight insect-plant interactions (Table 8.1)

Experiments on the effects of elevated CO_2 on insects have been carried out using plants grown in either greenhouses with no temperature or light control, growth chambers with varying degrees of temperature control and full or partial artificial lighting, or in open-topped chambers, where plants were subjected to fluctuating temperatures (Watt *et al.*, 1995). In most studies, plants have been exposed to two CO_2 concentrations, one at, or approximating to, ambient (usually around 350 umol mol^{-1}), and another at elevated CO_2, in the range 650 to 700 μmol mol^{-1}.

Until recently, most studies on the effects of elevated CO_2 on insect performance have involved the use of excised plant material inside petri dishes or similar containers. However, recent studies have been done with insects caged on whole plants (Watt *et al.*, 1995; Docherty *et al.*, 1997a). Several aspects of insect performance have been studied. Most experiments have included some measure of

Table 8.1.Studies on the impact of elevated CO_2 on tree-feeding insects

Insect species	Tree species	Reference
Lymantria dispar L. and *Malacosoma disstria* Hbn.	*Populus tremuloides* Mich., *Quercus rubra* L. and *Acer saccharum* Marsh.	Lindroth, Kinney and Platz, 1993
Lymantria dispar L.	*Betula papyrifera* Marsh. and *Pinus strobus* L.	Roth and Lindroth, 1994
Hyalophora cecropia L. *Actias luna* L. and *Antheraea polyphemus* Cram	*Betula papyrifera* Marsh.	Lindroth, Arteel and Kinney, 1995
Operophtera brumata	*Picea sitchensis* (Bong) Carr., *Acer pseudoplatanus* L., *Fagus sylvatica* L.	Watt *et al.*, 1996
Panolis flammea and *Neodiprion sertifer*	*Pinus contorta* and *Pinus sylvestris*	Watt *et al.*, unpublished
Rhynchaenus fagi	*Fagus sylvatica* L.	Docherty *et al.*, 1996
Elatobium abietinum, Cinara pilicornis and *Cinara pinea*	*Picea sitchensis, Picea abies* and *Pinus sylvestris*	Watt *et al.*, unpublished (and this paper)
Drepanosiphum platanoidis, Periphyllus testudinaceus, Phyllaphis fagi, Fagocyba cruenta and *Ossiannilssonola callosa*	*Acer pseudoplatanus* and *Fagus sylvatica*	Docherty *et al.*, 1997b

larval growth, either weight gain, weight at a certain stage of the life cycle, or relative growth rate (RGR),

$$RGR = \frac{\ln(weight_2)-\ln(weight_1)}{(t_2 - t_1)}$$

where insects are weighed at the beginning and end of a period of growth (t_1 and t_2 respectively). The use of RGR (or MRGR) is particularly widespread in aphid studies because it is quick and easy to measure (Brown, 1995), and because RGR is closely correlated with r_m, the population rate of increase (Leather and Dixon, 1984), which is less easy to measure, even when estimated by the formula (Wyatt and White, 1977):

$$r_m = 0.74 \left(\frac{\ln F_D}{D}\right)$$

where D is the development time or number of days from birth to adult and F_D is the number of young born in D days.

Several studies have also considered insect survival, larval development rates, consumption rates, approximate digestibility and related measures of food utilization, and one study also examined the effect of elevated CO_2 on insect fecundity (Fajer *et al.*, 1991). In addition, direct measurements of insect abundance and rates of increase were made in a few studies (Watt *et al.*, 1995).

Experiments on spruce aphids: materials and methods

During 1993-95, experiments were carried out at ITE Edinburgh on *Elatobium abietinum, Cinara pilicornis* and *Cinara pinea.*

Three host plants were used in the experiments: Sitka spruce (*Picea sitchensis*), Norway spruce (*Picea abies)* and Scots pine (*Pinus sylvestris*). Two-year old trees were placed in open-top chambers (OTCs) (Murray *et al.*, 1994), four at ambient and four at elevated CO_2 (700ppm). Experiments were carried out as follows:

a) *E. abietinum* on Norway spruce (1993, 1994, 1995),

b) *E. abietinum* on Sitka spruce (1993),

c) *C. pilicornis* on Norway spruce (1994),

d) *C. pinea* on Scots pine (1993, 1994).

In each case, aphids were caged singly from birth and their growth rates measured as described above. Generally two aphids were reared on each tree but if both aphids survived, their growth rates were averaged to give a single value for each tree. For each experiment, aphids were reared on five trees in each chamber, and, each year, experiments were repeated at least twice. The data were analysed by nested (trees within chamber) analysis of variance, pooling the data from the experiments carried out each year. The total number of growth rate observations for each analysis is given with the statistical details below.

Experiments on spruce aphids: results

a) *E. abietinum* on Norway spruce

There were no significant differences between the growth rate of *E. abietinum* on Norway spruce at ambient and elevated CO_2 in 1993 (F=0.29, observations=63, d.f.=1, *P*=0.61) or 1994 (F=5.77, observations=92, d.f.=1, *P*=0.053), although it is notable that the 38% decrease in growth rate in elevated CO_2 in 1994 is very close to being statistically significant (Figure 8.1). Insufficient data were collected in 1995 for statistical analysis but analysis of the data collected over the three years showed that elevated CO_2 had no significant effect on this species on Norway spruce (F=2.21, observations=177, d.f.=1, *P*=0.17).

b) *E. abietinum* on Sitka spruce

On *Picea sitchensis*, the growth rate of *E. abietinum* was not significantly affected by elevated CO_2, although a (3-38%) non-significant increase in growth rate occurred in elevated CO_2 in trees with and without the addition of fertilisers (F=3.01, observations=80, d.f.=1, *P*=0.13) (impact of nutrients: F=1.89, d.f.=1, *P*=0.22) (Figure 8.2).

c) *C. pilicornis* on Norway spruce

The growth rate of *C. pilicornis* on Norway spruce was not significantly affected by exposure to elevated CO_2; a non-significant decrease (of 33%)

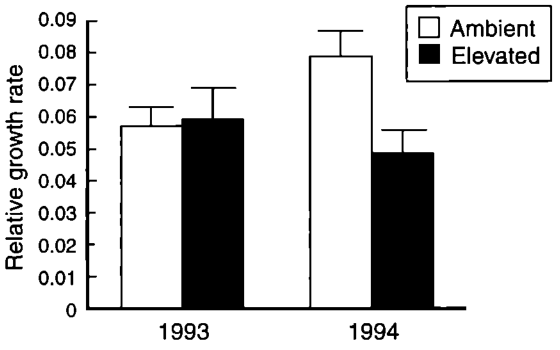

Figure 8.1 Effect of elevated CO_2 on growth rate of *Elatobium abietinum* on Norway spruce.

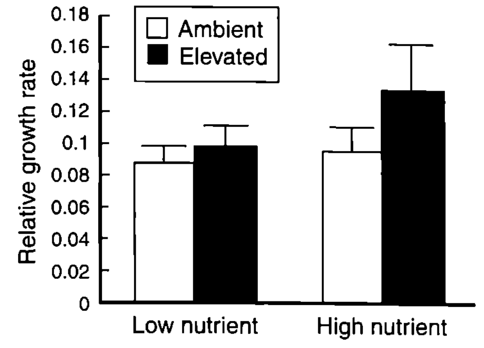

Figure 8.2 Effect of elevated CO_2 on growth rate of *Elatobium abietinum* on Sitka spruce.

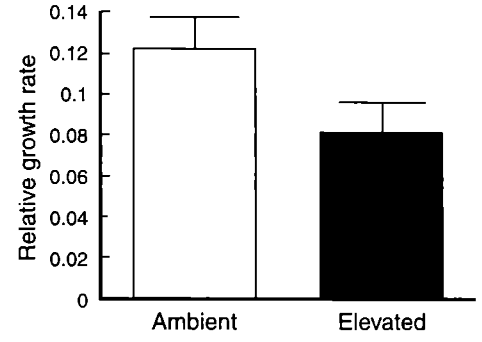

Figure 8.3 Effect of elevated CO_2 on growth rate of *Cinara pilicornis* on Norway spruce.

in growth rate was recorded in the one year in which this species was studied (F=2.02, observations=81, d.f.=1, *P*=0.21) (Figure 8.3).

d) *C. pinea* on Scots pine

In both 1993 and 1994 a small non-significant decrease in growth rate of *C. pinea* (1993 1% increase, 1994 29% decrease) was recorded on Scots pine (1993, F=0.21, observations=15, d.f.=1, *P*=0.67; 1994 F=0.29, observations=34, d.f.=1, *P*=0.61; 1993, F=0.03, *P*=0.87) (Figure 8.4).

Discussion and conclusions

Previously unpublished results presented here on the impact of elevated CO_2 on the performance of *E. abietinum* and other conifer aphids suggest that elevated CO_2 has a small negative, but statistically insignificant, impact on aphid growth rate (Figures 8.1-8.4). Only the results on *E. abietinum* on Sitka spruce suggest that elevated CO_2 can have a positive effect on aphid growth rates (Figure 8.2).

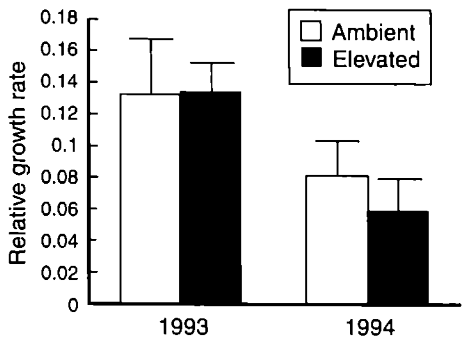

Figure 8.4 Effect of elevated CO_2 on growth rate of *Cinara pinea* on Scots pine.

Taken together with other published and unpublished studies on the impact of elevated CO_2 on insects feeding on tree foliage, most of the experimental data suggest that elevated CO_2 has no impact, or a small negative impact, on insect performance (Figure 8.5). However, it is notable that few of the experiments carried out to date have reported statistically significant results and therefore any discussion of these results must be tentative. A comparison of the results of experiments on leaf-chewing and leaf-sucking insects shows that of the ten experiments on leaf-chewing insects eight showed that elevated CO_2 had a negative impact on growth rate, but of the same number of experiments on leaf-sucking insects six showed that elevated CO_2 had a negative impact on growth rate (Figures 8.6-8.7). However, the respective average impacts of elevated CO_2 - 15% among leaf-chewing insects and -10% among leaf–sucking insects, the small number of studies on each group of insects, and the general lack of statistical significance do not provide convincing evidence for a difference between leaf-chewing and leaf-sucking insects, on trees at least.

The results of experiments on the impact of elevated CO_2 on spruce aphids and other forest pests suggest that climate change will not affect their status as pests greatly. However, increasing atmospheric CO_2 is only one aspect of climate change. The question of whether increasing global temperatures will affect forest pests is outwith the scope of this chapter. However, increasing temperatures are likely to affect insect pests in many ways. Some of these effects will be negative, such as the disruption to insect-plant synchrony (Dewar and Watt, 1992), but the overall impact on forest pests is thought to be positive to the degree that it has been predicted that forest pest problems will spread as the climate changes (Fleming and Volney, 1995; Williams and Liebhold, 1995).

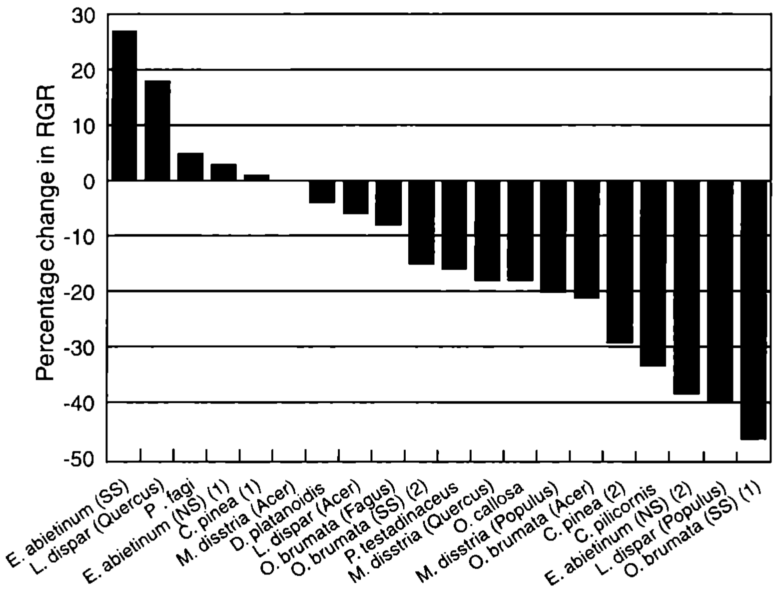

Figure 8.5 Effect of elevated CO_2 on relative growth rate of insects on trees.

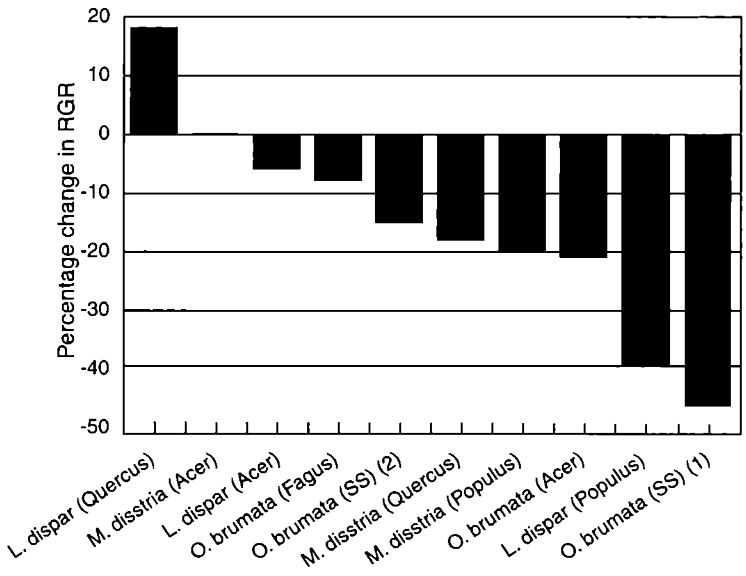

Figure 8.6 Effect of elevated CO_2 on relative growth rate of leaf-chewing insects on trees.

As pointed out elsewhere climate change is only one aspect of global change (Lawton, 1995; Watt *et al.*, 1995, Docherty *et al*, 1997a). The status of forest pests is also susceptible to pollution and many other factors. Taking *Elatobium abietinum* and *Cinara pilicornis* as examples, recent experimental research has shown that exposure to SO_2 and NO_2 leads to an increase in aphid performance, the effect of exposure to ozone is different for each species, and elevated CO_2 has no significant effect on either species (Table 8.2). These results are typical of most species studied. In conclusion, therefore, elevated CO_2 is unlikely to change the abundance of spruce aphids and other forest pests to a significant degree, but the effects of atmospheric pollution and global warming are such that the threat of aphids to forest trees may increase in the predicted future climate.

Where should research be directed now?

1) Despite the amount of research over the last few years, we still have a very poor understanding of the magnitude of the effects of elevated CO_2, SO_2, NO_2 and ozone on insect pests. The impact of ozone in particular is very poorly understood. Thus more experiments on single pollutants are required. These experiments should include more species, be of longer duration than most experiments carried out to date and include more than the measurement of RGR, no matter how easy.

2) Research on the effects of ozone at different temperatures (Brown *et al.*, 1993), and SO_2 on droughted and well-watered plants (Warrington and Whittaker 1990) demonstrate that interactions between different factors require much more attention, despite the

Table 8.2 The effects of pollutants and CO_2 on *Elatobium abietinum* and *Cinara pilicornis*

a) Effects of pollutants and CO_2 on *Elatobium abietinum*

Gas	Host plant	Impact of exposure
SO_2	Sitka spruce	increase in RGR and abundance (McNeill *et al.*, 1987; Warrington and Whittaker, 1990)
NO_2	Sitka spruce	increase in RGR (Brown *et al.*, 1993) - up to 55%
O_3	Sitka spruce	no significant effect on RGR (Brown *et al.*, 1993)
CO_2	Norway spruce	no significant effect on RGR
CO_2	Sitka spruce	no significant effect on RGR

b) Effects of pollutants and CO_2 on *Cinara pilicornis*

Gas	Host plant	Impact of exposure
SO_2	Norway spruce	increase in abundance (Holopainen *et al.*, 1991, 1993)
NO_2	Sitka spruce	increase in RGR (Brown *et al.*, 1993) - up to 20%
O_3	Sitka spruce	increase in RGR at low temperatures, decrease in RGR at high temperatures (Brown *et al.*, 1993)
CO_2	Norway spruce	no significant effect on RGR

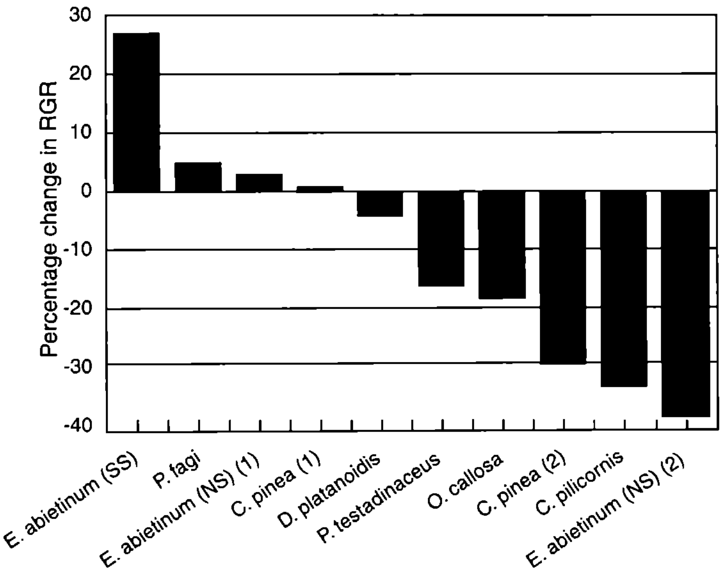

Figure 8.7 Effect of elevated CO_2 on relative growth rate of aphids and other sap-feeding insects on trees.

complexity of the experiments required to study two or more factors. The degree to which we have to think about the way that pollutants interact with other factors is well demonstrated by Neuvonen *et al.*, (1990) who reported that the susceptibility of *Neodiprion sertifer* to nuclear polyhedrosis virus was reduced by simulated acid rain

3) The biochemical basis for the effects of elevated CO_2 is reasonably well understood, at least for leaf-chewing insects, but the biochemical bases for the effects of pollutants are unclear, despite some recent comprehensive studies (e.g Kainulainen *et al.*, 1993). Much more emphasis should be put on this aspect not least because it could provide a scientific basis for the effects of different pollutants and their interactions.

4) Finally there is a need to place the results of experiments in the correct context, i.e what do the results mean for the abundance and damage done by insect pests. First this requires a change in the approach to experiments. Although they produce less clear results than closed-chamber experiments, field experiments and gradient studies (e.g. Holopainen *et al.*, 1993) can provide an understanding of how the effects of pollutants

on individuals are manifest on populations, which are already affected by a range of density-independent and density-dependent factors. Few field studies have, to date, measured the impact of natural enemies, but Holopainen *et al.*, (1993) showed that differences in the abundance of *Cinara pilicornis* along a SO_2 gradient were unlikely to be due to natural enemies by monitoring the abundance of predators and the rate of parasitism. In addition, there is a need for more modelling studies such as that carried out by Kidd (1991)

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Chapter 9

Prospects for sustainable management of forests to minimise the green spruce aphid problem in Europe

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Contemporary interpretation of the relationship between the pest and its forest environment

The green spruce aphid, *Elatobium abietinum*, is now recognised as a significant component in the plantation forestry system of western Europe. Its real status as a forest pest, that is its potential to reduce the productivity of the forest environment, has remained in question until recently despite its evident capacity to cause widespread and periodic defoliation in most areas where Sitka spruce (*Picea sitchensis)* is grown. The evolution of its pest status can generally be attributed to the following:

1. planting of Sitka spruce, one of the most susceptible hosts, has increased in recent years
2. the climate of areas conducive to high growth potential in Sitka spruce, is particularly favourable for aphid survival and population development.

If *E. abietinum* was originally an aphid associated with *Picea abies* in Europe (Chapter 1), then it has since been introduced as an exotic species to many other parts of the world where suitable host plants exist. The aphid appears to have become a major problem in New Zealand, and is increasingly evident in natural stands of Sitka spruce, in seed orchards and in plantations of other spruce species along the west coast of North America.

Research in Europe has demonstrated that severe infestations of *E. abietinum* have a significant and protracted effect on spruce growth. Recent studies have characterised this response for young trees, but the response of older trees in plantations is less well documented and may be different (Chapter 2). Modelling studies have started to use the empirical information available to estimate impacts on final tree sizes and yields and these suggest that growth losses might be greater during the latter half of the forest rotation (Chapter 3). Model simulations also indicate that repeated attacks over the life of the crop are capable of reducing timber yields significantly.

Population dynamics

Aphid populations undergo dramatic temporal changes and there is also a spatial component to their population dynamics which is determined by climate. Chapter 4 summarises the recently published studies which have attempted to characterise the underlying causes of change and stability in *E. abietinum* populations and the thermal constraints imposed on population growth, particularly in severe winters. While population studies on their own provide few pest management solutions, they are the tools with which predictions of economic impact can be made and they allow further investigation of ways in which the abundance of the pest might be suppressed. Simulation models are particularly good at allowing the exploration of the possible effects of management options. They therefore provide a vital link between studies of the impact on tree growth and the measures which may be introduced to reduce that impact. Current work indicates that useful insect population models for management, based on sufficient biological understanding, could be derived from much existing knowledge (Chapters 4 and 6)

Cultural and genetic components of resistance

In contrast to many other insect pests, *E. abietinum* does not appear to be favoured by reduced vitality of its host trees. Rather, aphid attacks occur most intensely on the trees which are showing the best growth within a seed origin; good nutritional status and fertilisation with nitrogen often but not always promotes aphid population development. This means that, unlike the management of other insect pests, the management of the green spruce aphid, cannot focus on the improvement of tree vitality through silviculture as a measure to ameliorate damage.

It seems that both cultural and genetic components influence either the ways in which aphid populations develop on trees or the manifestation of their effects. It is noticeable that trees within a forest stand are differentially attacked (mainly genetically determined), and that different stands within close proximity can be affected in different ways. Such differences often result from cultural factors possibly modified by microclimatic variation. Differences in susceptibility have been demonstrated at species, provenance, family and clonal levels (Chapter 7) and the understanding of the extent and heritability of resistance to the green spruce aphid is gradually increasing as studies of genetically defined host plants are intensified (Chapter 7). However, although the visual expression of differential susceptibility is obvious, the underlying mechanisms of resistance are still only poorly understood.

The same applies to the influence of cultural factors on the effect of aphid attack on spruce and only a few studies have been carried out to elucidate the effects of physicochemical properties of the soil on aphid attack level and of the implications of silvicultural practice. Nutrient supply positively affects aphid population development, but interactions between nitrogen (N) and other nutrients such as K, Cu and Mg, commonly used in fertilisation programmes, most likely exist (Carter and Nichols, 1985), but have so far not been thoroughly investigated. The role of nutrient availability in the aphid-tree system depends on the underlying cause of nutrient imbalance. Where scarcity of N is the problem, lower foliar N concentration would be expected to be detrimental to the spruce aphid and lead to smaller populations. Where other nutrients are limiting and N remains relatively abundant, then higher aphid populations might develop particularly if chemical imbalance within the tree leads to higher than normal concentrations of N, greater availability of key amino acids and reductions in defensive chemicals. Such patterns are poorly researched at present although a partly experimental approach to this problem by Thomas and Miller (1994) found no evidence that elevated inputs of N (or P), from whatever source, lead to increased sensitivity to aphid damage. However, interactions between spruce aphid attack and particular types of nutrient stress may exacerbate tree decline, as perhaps has occurred on some sites studied in South Wales (Coutts, 1995).

The green spruce aphid may have a role in long-term nutrient cycling in forest ecosystems. This role may in the short term be beneficial, but may eventually be detrimental to spruce growth and productivity. In Denmark, studies have shown that faecal droppings from insectivorous birds (Paridae), which occurred in markedly increased numbers in heavily infested stands, add nutrients to the soil so stimulating tree growth. These droppings contain large amounts of P, N and K. The carbohydrates from aphid honeydew lead, together with the nutrients, to increased decomposition in the forest soil. The rise in temperature resulting from the increase in light penetration after heavy defoliation also leads to an increased activity of microorganisms. Decomposition may be so intense that the result is a great washout of N as nitrate. The creation of these high nitrate levels is followed by an acidification of the forest soil. It has also been observed that P, N and K, and dissolved organic matter, leach more rapidly from damaged needles. About 50% of the total depletion of P and K happened in May and June when these substances are important to the vitality of the trees. The main problem is considered not to be the additional loss of nutrients but the timing of loss (Pedersen, 1992).

Predators and parasitoids

The fact that extensive defoliation of spruce can occur, even in the presence of diverse natural enemy populations, encourages opinion that enemies play little part in governing population size of the pest. However, evidence is emerging that biological controls could be important in minimising damage at certain times of the year (Chapter 6) and where population growth rate of aphids is slowed by tree resistance mechanisms (Chapter 7) or climate, thus reducing the effects of predator-prey functional responses and improving the numerical responses of enemies to changing aphid population densities. The decisiveness of their effects might vary regionally, perhaps in accordance with the large differences which exist between the natural enemy faunas of different forests. These differences are most marked when comparison is made between Iceland and other regions of oceanic northwestern Europe (Chapter 5). Only a few of the natural enemy species normally found in forests of northwestern Europe, have been found in Iceland. None of the Coccinellidae, Hemerobiidae, Anthocoridae or Araneida and only one of the Syrphidae were found in systematic surveys (Austarå *et al*, 1997). In Iceland too, an aphid population peak frequently occurs in late autumn or early winter, and models developed in Chapter 4 support a link between this phenomenon and the absence of natural enemies. Of course the thermal environment, which so firmly underpins aphid developmental rates, is also very important in Iceland. Thus, a regional comparison, while lacking critical experiments, may provide some insight into the important role played by enemies in the aphid's main areas of distribution. Models developed in Chapter 6 are generalised tools which can provide the basis for further examination of the contribution made to aphid population dynamics by most aphid predators or parasitoids. Since the models provide testable hypotheses, there is every reason for using them in conjunction with field and laboratory observations and experiments.

Pathogens

Fungal pathogens from the Entomophthorales are pervasive in some high density populations of aphids and may require specific environmental conditions to become epidemic. The need for critical conditions is suggested by their occurrence, which is spatially and temporally sporadic. Six species have been found in western European regions, while *Neozygites fresenii* is the only one found in Iceland (Chapter 5). Their occurrence has been estimated in some studies as a percentage of aphids in samples, which show definite signs of lethal fungal infection or as proportions of aphids *destined* to develop infection and die, demonstrated by careful rearing and diagnosis of prevalence. Only the latter method is a reliable indicator of the killing power of entomopathogens, but it is time consuming and results of this quality have not been obtained fully in a systematic way. It can however be concluded tentatively that entomopathogens make a significant contribution to keeping summer peak aphid population levels below their highest potential.

Climate change and pollution

Gaseous air pollutants, especially SO_2 and oxides of nitrogen, generally enhance the performance of herbivorous insects, especially aphids, by inducing a stress reaction in the host plant that increases the availability of soluble nitrogen within the plant tissues. Nitrogen is the most important nutritional chemical for insects. Increased individual performance on plants exposed to pollutants leads to higher populations of *E. abietinum* and hence greater impact (Chapters 2 and 8). Wet deposition of SO_2 and NO_x as acid rain may, especially in the case of the latter, increase nutrient availability to forest trees and improve growth, especially on sites where nitrogen is limiting. Deliberate fertilization has the same effect, but improvements in plant nutritional status by either mechanism also, tend to increase foliar nitrogen concentrations and promote higher aphid populations. Faster growing, fertilized trees have been observed to suffer higher rates of infestation and defoliation, and greater relative growth losses (Chapters 2 and 7). However, whether the direct improvement in growth is sufficient to outweigh the effects of greater susceptibility to infestation is far from certain.

The influence of gaseous air pollutants on aphid populations is likely to be rather localized and in general is considered to be decreasing in north western European countries (Brown, 1995). In contrast, CO_2 concentrations in the atmosphere and associated changes in mean annual temperatures operate at a global scale and are set to continue to rise. CO_2 appears to have little direct influence on insect performance, at the most a small negative effect (Chapter 8), whereas increased temperatures are likely to benefit many insect species by speeding up developmental rates and enhancing reproductive output. *E. abietinum* is especially likely to respond to milder winter weather, since a reduction in the chances of severe or prolonged freezing will allow more individuals to survive until the spring, enabling higher peak densities to be achieved (Straw, 1995). However, warmer temperatures are also likely to benefit natural enemy populations. Consequently, the net effects of global climate change for *E. abietinum*, and populations of other insect pest species, are difficult to predict (Harrington *et al.*, 1995).

The influence of drought (water stress) on spruce and on the dynamics of spruce aphid populations, and on impact, is poorly understood. Climate change may induce more frequent summer droughts in areas relatively marginal for growing Sitka spruce, and interactions with spruce aphid may exacerbate or ameliorate this effect. Current information on the effect of drought is mixed. Warrington and

Whittaker (1990) indicated that drought had a large direct effect on the plant but no interaction with the green spruce aphid, whereas Major (1990) found that intermittant drought stress increased aphid population densities. More systematic studies are required to elucidate typical responses.

Prospects for sustainable management and research needed in the future

The green spruce aphid can be killed by pesticides, indeed this is an option used by Christmas tree growers (Carter and Winter, 1998), but it is not considered a sustainable means of regulating the pest nor is it likely to be good for the integrity of a forest plantation environment, even in the short-term. The management of the aphid in future will rely more heavily on developing resistance in forest trees through tree-breeding or silviculture, and combining this with augmentation of biological controls. A framework for achieving cost-effective management will be built on flexible models for the aphid-tree system and a better knowledge of the impacts of the insects on tree growth. The effects of climate change and pollution are external factors that deserve continued study, given the long-term nature of forest economics. A final consideration is the genetic basis for aphid bionomics and how this affects the pest problem in existing and new parts of its range.

Resistance or susceptibility?

The most promising way in which green spruce aphid effects will be minimised in future will be through improving resistance in plantation stock. Although variation has been found at provenance level, choice of provenance alone may however not be the only way forward in genetic management of the aphid, as a substantial and highly significant within-provenance variation has been demonstrated (Chapter 7). Genetically better-defined stock, i.e. families or even clones with a high degree of resistance are certain to be found within all provenances - a fact that give excellent prospects for improving resistance in different European regions. It may be necessary to improve stock from a wide range of seed origins since climatic constraints imposed on the host plants vary so much.

An important feature of resistance is that it is heritable, and recent analyses of resistance in progenies of Sitka spruce have shown a high family heritability (Chapter 7). Great family variation (in combination with high heritability) means that very high gains can be expected from selection for resistance. Selection for a specific trait may, however, create problems because of interactions with other traits for which selection is also demanded and between which a negative correlation may appear. So far there have been no negative relationships between resistance and growth parameters suggesting that high yield and resistance may be compatible goals. Investigations of interactions between resistance and other traits such as susceptibility to other pests or to cultural or climatic factors (e.g. frost tolerance) is obviously needed in the future before incorporating aphid resistance into breeding programmes.

Although it is evident that differential susceptibility is exhibited by individual spruce species, the mechanisms involved are still not fully understood. To evaluate the full scope of long-term benefits of improving resistance in the plantation stock, a clearer understanding of these mechanisms is required.

Firstly, comparative studies of aphid behaviour and performance on susceptible and resistant host plants should be undertaken to examine whether resistance is connected with the colonisation and establishment phase of the aphids (antixenosis), or if the resistance mechanism is antibiotic in nature, operating negatively on survival, development and/or reproduction. Furthermore, although studies have comprised aphid counts and assessments of defoliation, only a few observations exist on both parameters on the same plants which would permit a better understanding of the degree of tolerance of different spruce individuals. Tolerance would imply that the plants in question are able to host a higher number of aphids without suffering as much as susceptible plants in the same circumstances.

Having identified individuals with a well-defined level of resistance a second step in the identification of mechanisms responsible for resistance will be to analyse in detail the characteristics of the resistant genotypes. In the first place it will be useful to search for not only chemical components, mainly terpenes and phenolics, which are known to play an important role as plant defence substances, but also anatomical features of the needles. The ability to identify specific host plant characteristics connected with resistance would eventually aid in developing methods for screening plant material as early as the nursery.

Screening should however be based on the assumption that resistance is fairly consistent in time. To some extent it is always modified by abiotic and biotic factors, but the general level of resistance should not vary substantially with the age of the trees. Therefore, long-term studies of the consistency of resistance are badly needed. In turn, studies of the heredity of resistance with the objective of determining its genetic basis are also important. Here two approaches are appropriate; the first comprises the calculation of genetic parameters such as estimates of broad sense and narrow sense heritability. Genetic variation within and between genetically defined spruce material should be further investigated and determined and estimates of genetic correlation between aphid resistance and other traits would allow an evaluation of the scope for breeding for resistance. Another approach should be directed at DNA analysis, focusing on determining the presence and expression of different resistance-associated genes.

There is a perceived danger in applying the results of plant breeding, which is that resistance will eventually be broken by the pest and the entire defensive strategy of a commercially-grown species will be penetrated. We believe that the prognosis for Sitka spruce in relation to the green spruce aphid is more promising than this for the following reasons. Firstly, *E. abietinum* is almost exclusively anholocyclic in regions where it poses the greatest challenge to Sitka spruce (Carter and Austarå, 1994), and therefore its anticipated evolutionary rate should be correspondingly slow. It should therefore be relatively slow to adapt to genetically based resistance in its host plants. Secondly, the apparent stability of resistance within Norway spruce *(Picea abies)* (the likely original host of *E. abietinum*, Chapter 1) suggests that, once established in a population of trees, resistance to the aphid is not so easily penetrated in evolutionary time. Within the genetic variability of Sitka spruce it should be possible to identify resistance traits comparable to those in Norway spruce, and to expect them also to have long-term stability.

Biological controls

There is little doubt that natural enemies could contribute significantly to preventing the development of high aphid population densities. However, research is only beginning to understand the true impact of predators and parasitoids on the green spruce aphid, and there is no consistent data for the impact of pathogens. Ways of augmenting natural enemies, their biodiversity and their impact, should now be developed more systematically.

The existence of variable predator communities and sporadic occurrence of pathogens suggests scope for managing the forest environment to gain the best advantage from their presence. As a first measure, structured quantitative samples of natural enemy communities are needed from forests to relate the presence of key taxa or the biodiversity of natural enemies, to forest environmental variables. A clearer understanding of the geographic and silvicultural limitations to natural enemies is required.

As a second step, there is a need for a better understanding of the impact of natural enemies on the pest. Information exists for some species in only two published studies (Chapter 6). Ideally, there should be structured age-specific demographic data for all the important species in a locality, in order to construct flexible sub-models of the natural enemy effects (Barlow and Dixon, 1980). Since this is not achievable for all forest and climate systems in western Europe, a number of inferences will have to be made and the outcome of the simulation modelling tested against as many data sets as possible from field (forest) populations of aphids.

Taking a lead from a knowledge of insect and pathogen biodiversity patterns, there should also be studies relating the most important natural enemies to specific features in forests which could act as reservoirs or provide alternative resources. The existence of alternative prey species for aphid predators (Parry, 1992) could be a crucial element in sustaining effective population levels. Alternative habitats may provide a similar opportunity for predators, parasitoids and pathogens and could be investigated with their juxtaposition to forests in mind. Some alternative habitats could even be created within spruce stands. This kind of approach has been considered by Dennis and Fry (1992) and Dennis *et al.* (1994) for predatory arthropods inhabiting field margins in agricultural landscapes. Forest stand edges have a particular character which can influence the ecology of insect pests (Peltonen *et al.* 1997) and through fragmentation of forest units, are known to influence their dynamics (Roland, 1993). There are therefore options in forest design and mosaic structure which might be relevant to reducing critical levels of the pest. Many of these ideas are resonant with European and national policies on forestry, which now seek to increase the biodiversity of commercial plantations and to improve the conservation potential of such habitats (Anon., 1995).

The four most frequently encountered fungal species pathogenic to *E. abietinum* are also those found commonly on field crop aphid pests, and in fact on a wide range of aphid species. For pathogens there are almost certain to be reservoirs in areas surrounding forests. Possibly even more important are habitats within the forest dominated by woody or herbaceous plants which in turn are inhabited by other aphid species acting as fungal reservoirs when the spruce aphid population is low in summer (Steenberg and Eilenberg, 1995). This may be especially relevant to Iceland where many potential natural enemies are absent but there are at least experimental forest systems with spruce, lupin and birch. The common aphids on birch *Betulaphis quadrituberculata* and *Euceraphis punctipennis* may share natural enemies with *E. abietinum*. Once again it should be emphasised that detailed empirical and modelling studies of natural enemy and pest interactions will chart the way for management options.

Models of population dynamics

Simulation modelling is a useful way of overcoming the problems which arise because aphids have overlapping generations and rapidly changing age distributions. The usefulness of such models is that they can integrate most available knowledge, provide a functional basis for observed events and a stringent test of understanding, show precisely where future work is required and provide a framework into which it can be incorporated, and increase understanding of the roles of interacting component processes (Barlow and Dixon, 1980). This approach has worked particularly well for other tree-dwelling aphids for which the egg stage provides a convenient end-of-season point of reference and by means of which insect populations in consecutive years can be linked by observation and model output. In the areas of its European range in which we are interested, the green spruce aphid is anholocyclic and often declines to imperceptibly low population levels during the winter, making it difficult in turn, to link simulations effectively from one year to another. So far, simulation modelling has illuminated the roles of processes which govern the increase and decline in population within a year, while the analysis of population time series by multiple regression has shed some light on year to year changes in aphid peak numbers (and hence foliar damage to spruce). Thacker (1995) and others (Chapter 4) have deployed a variety of available data on *E. abietinum* populations (indices and counts) in analysis of the relative strengths of regulation and weather factors in determining the pattern of population change and stability.

The importance of the thermal environment has long been recognised but only recently quantified sufficiently to allow an attempt at regional analysis of aphid attack probability. With sufficient local thermal data this could be progressed to the stage of a green spruce aphid risk assessment for European forests. This could either be used in its own right to indicate to forest research organisations the attention this aphid should merit, or it could overlay the regional cost-benefit prognosis which would take into account measures to introduce resistance and augment biocontrols and to set these against the likely impact of aphid attack.

Impacts

Assessing the costs and benefits of introducing resistant spruce genotypes and efforts to augment biocontrols depends crucially on having a clear description of the relationship between aphid densities, defoliation and impact on tree growth. The relationship between the pest and its economic costs over the life of a crop is not a simple one and can be defined only by a combination of experimental studies, retrospective investigations and plantation-scale growth modelling. It is essential in this work, especially for empirical studies, that growth losses are related to accurate measures of aphid density and needle loss, not only to define the key relationships, but also to ensure compatibility between studies conducted in different regions and different phases of the forest cycle.

Ultimately, modelling studies are the only means by which the effects of separate aphid outbreaks can be integrated to predict impacts on final tree size and plantation yields. Reliable predictions depend on the models simulating the effects of aphid attack accurately and hence they must calibrate against empirical data. However, certain basic information is still unavailable, particularly the response of older trees to infestation and the number and severity of outbreaks that stands typically experience during their lifetimes. Current models also require better parameterisation to incorporate seasonal differences in the pattern of aphid attack and foliar phenology within years, and better representation of within crown defoliation patterns.

Preliminary results with the growth model GROMIT indicate that a small number of aphid outbreaks or only light defoliation have little effect on long-term growth. Consequently, it may be possible to identify a rate of defoliation, or aphid infestation, below which impact on growth is tolerable and toward which management of the pest could be targeted. Estimates of growth losses caused by frequencies of outbreaks and rates of defoliation above the economic threshold could inform decisions on whether to delay harvesting to compensate for reduced growth and be used to evaluate the costs and benefits of pest management options. Knowing the relationship between aphid populations and defoliation, and the effects of defoliation on increment, should allow models of aphid population dynamics and stand performance to be combined, to predict how stand yield class relates to higher or lower aphid populations, for different types of sites and in different regions and, in the longer term, how productivity of Sitka spruce may fall if spruce aphid populations increase because of climatic change. An estimate of the future yield class of Sitka spruce would indicate when the planting of alternative crop species might become as economically attractive.

Abiotic Influences

Despite the research over the last few years, we still have a very poor understanding of the magnitude of the effects of elevated CO_2, SO_2, NO_2 and ozone on insect pests. The impact of ozone in particular is very poorly understood, even though this pollutant operates more regionally and is steadily increasing in importance. The effects of ozone appear to be modulated by temperature and the effects of other pollutants also appear to be modified by other factors (e.g. SO_2 and drought). Hence more attention needs to be given to experiments that explore interactions between pollutants and between these and other environmental variables. The biochemical and physiological processes that modify the effect of pollutants are also unclear. An understanding of these would provide a scientific basis for the effects of different pollutants and their interaction. A further requirement is that experimental results need to be taken from the laboratory and tested in the field to determine effects on populations.

Pest variability

Are lineages of aphids from different regional or host sources biologically different (Blackman, 1979, 1980), in a way which has real consequences for predicting the outcome of the environment-aphid-tree interaction? A first step to answering this question is to identify the genetic diversity within and among populations in northern and western Europe and to determine the importance of this diversity to the performance of the aphid on different plants and to its tolerance to adverse climatic conditions. Some progress with this is currently being made in Iceland (Sigurdsson *et al.*, 1998) where the relatively recent introduction of the green spruce aphid has a special significance (Chapter 1) The approach is an analysis of aphid DNA by the RAPD method to characterise aphid lineages from selected geographic and host origins. Molecular measures have been extended to improve accuracy and provide better resolution of genetic relationships among aphids. Previous work has been designed around RAPD markers, but it would now be desirable to use two additional types of markers: 1) RFLP analysis using a major ribosomal gene (rDNA), and 2) a satellite sequence. These approaches will tell us more about the molecular nature of the mutations or genetic differentiation while RAPD is based on random amplification only.

Initial results from the analysis of genetic variation using the RAPD method show that the Icelandic population of the green spruce aphid is very homogeneous (Sigurdsson *et al.*, 1998). Only two clones have been detected in a geographic area ranging from the west coast south to the eastern fjords. No variation was detected within each site where aphids were sampled directly from trees, and there was a clear geographical line between these two clones which divides them between (1) the west and south of the country and (2) the east. The responses of these two clones to host plants of differing quality remain to be seen, but it may be speculated that the introduction of resistant planting stock will be at least as successful in Iceland as elsewhere, if not more so since the aphids have a low genetic diversity. To retain this advantage, the strict controls on importation of futher live aphid material to Iceland should be maintained. Genetic variation of the green spruce aphid has also been investigated in New Zealand (Nicol *et al.*, 1998). Here there is no detectable genetic variation, compared with high variation among populations sampled in the United Kingdom.

A range of work in which there is further analysis of samples from other countries using both RAPD and other marker aided methods should be progressed. There need to be parallel studies of the population growth, performance and tolerance of defined aphid lineages to sub-zero temperatures, and of course to spruce of different genetic origin.

Final observations

There is a need to combine a knowledge of all these elements to produce practical recommendations for IPM (Integrated Pest Management) to be applied at the European scale. Some recommendations have arisen from within the European Community Concerted Action (AIR3-CT94-1883) and are reported in earlier Chapters in this volume, but for the most part the Action has enabled a harmonisation of activities and provided an international impetus for future research which will achieve an IPM goal. Over the next few years it is anticipated that there will be integration of results accomplished under the headings of resistance and biocontrol, and a summary of economic predictions for forest growth, with and without forest protection improvements. The likelihood that the effect of tree resistance will reduce aphid population growth rate and improve the efficacy of natural biological control agents, is keenly anticipated.

Models need development so that we have greater confidence in their ability to reflect management decisions, such as the introduction of more-resistant tree stock. They should also respond adequately to the variations in effect of natural enemies. The resulting spectrum of dynamical behaviour can then be directly linked to growth models in order to explore forest economics and the cost-benefit of different actions. It should be possible to tailor these outcomes for area-based prognoses. Models of the aphid sub-system will define risk areas in Europe and the integrated results on aphid differentiation and adaptation will enable us to say if introductions of the aphid to new areas will pose special threats to developing forestry. In the special case of Iceland, there may even be scope for measured introduction of some natural enemy species to improve biological control by the 'classical' route. As in New Zealand (Nicol *et al.*, 1998), the scope for this is increased by the relative genetic homogeneity of *E. abietinum* populations.

The consequences of the pest for tree growth are potentially serious, and becoming more so with anticipated environmental change. The aphid problem is a critical issue for developing forest industries in a number of countries where there is a heavy reliance on fast-growing timber species. The genetic gains obtained from planting propagated improved bulked family mixtures of Sitka spruce or stock from approved clonal seed orchards, can only be preserved by taking additional account of insect pests like the spruce aphid, since they can be associated with trees throughout an entire rotation.

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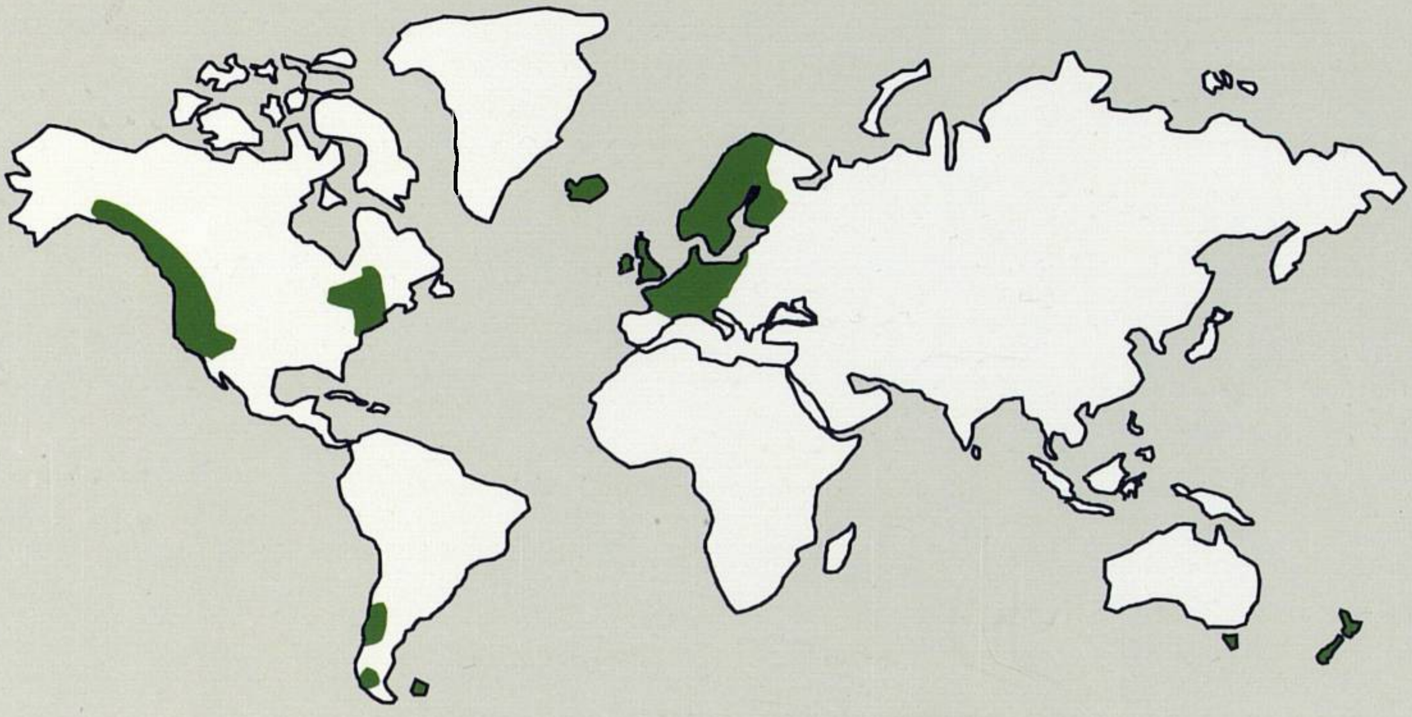

Known world distribution of the green spruce aphid, *Elatobium abietinum* (Walker)

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