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Variation in the abundance of invertebrate predators of the green spruce aphid *Elatobium abietinum* (Walker) (Homoptera: Aphididae) along an altitudinal transect

N.A. Straw [a,*], J.E.L. Timms [b], S.R. Leather [b]

[a] Forest Research, Alice Holt Lodge, Wrecclesham, Farnham, Surrey, GU10 4LH, UK
[b] Division of Biology, Imperial College London, Silwood Park Campus, Ascot Berkshire, SL5 7PY, UK

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ABSTRACT

Green spruce aphid *Elatobium abietinum* (Walker) is a major defoliator of Sitka spruce (*Picea sitchensis* (Bong.) Carr.) in north-west Europe and other parts of the world that have a mild and wet maritime climate. Periods of cold weather during the winter currently limit *E. abietinum* populations and the amount of damage, but as mean winter temperatures rise in response to global climate change, overwinter survival of the aphid is likely to improve and the risk of severe and more widespread defoliation will increase. Populations of *E. abietinum* are also influenced by mortality caused by generalist invertebrate predators, although the extent to which predation might modify the response of *E. abietinum* to climate change is unclear. In this study, the response of generalist predators to changes in environmental conditions and potential increases in *E. abietinum* populations was evaluated by sampling invertebrate predators in the canopy of Sitka spruce along an altitudinal gradient from 310 m to 610 m above sea-level. Variation in predator abundance was related to local climate and aphid numbers. Population densities of *E. abietinum* differed widely between altitudes, and showed different patterns in different years, but mean densities over the 3-year study were highest at mid altitudes. In contrast, the majority of invertebrate predators (coccinellid and cantharid beetles, syrphid larvae, brown lacewings, spiders and harvestmen) were most abundant at low altitudes. Their abundance was not correlated with *E. abietinum* densities, but coincided with the more favourable climatic conditions at low altitudes and the availability of alternative prey. The association of low population densities of *E. abietinum* with greater general abundance of invertebrate predators at low altitudes, where higher temperatures would have been expected to promote higher aphid populations, suggests that above a certain temperature regime generalist predators have the capacity to prevent *E. abietinum* responding to further increases in environmental temperatures and eventually cause mean population densities to decline. Consequently, increases in the activity and abundance of natural enemies need to be considered when predicting how *E. abietinum* might respond to climate change.

1. Introduction

Green spruce aphid *Elatobium abietinum* (Walker) is an important defoliating pest of spruce (*Picea* spp.). It is particularly damaging to spruce species of North American origin, which in response to infestation suffer extensive foliage yellowing and needle loss (Nichols, 1987). One of the most severely damaged species is Sitka spruce *Picea sitchensis* (Bong.) Carr., native to the west coast of Canada and the USA, but also planted widely as a commercial species in north-west Europe, Iceland and other parts of the world (Carter and Halldórsson, 1998; Halldórsson et al., 2003). Sitka spruce is one of the most productive tree species in these temperate maritime regions. The mild and wet climate that favours the tree's growth however, also suits *E. abietinum*, and allows it to persist as anholocyclic populations and to feed and reproduce on spruce throughout the year (Carter and Halldórsson, 1998). This combination of mild climate and inherent susceptibility to the aphid makes Sitka spruce particularly vulnerable to defoliation.

The aphid infests the 1-year old and older needle leaves (Jackson and Dixon, 1996). In the UK and adjacent parts of Europe, populations increase in the spring and peak during May or June (Parry, 1969; Day, 1984; Day et al., 2004). After the population peak, numbers decline rapidly in response to a decline in host

* Corresponding author. Tel.: +44 1420 22255; fax: +44 1420 23653.
E-mail address: nigel.straw@forestry.gsi.gov.uk (N.A. Straw).

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nutrient quality, and then remain low for the rest of the year. Defoliation by *E. abietinum* rarely causes tree mortality, but repeated infestation reduces growth and productivity (Thomas and Miller, 1994; Orlund and Austarå, 1996; Halldórsson et al., 2003; Straw et al., 2000, 2005). In other parts of the world however, notably in New Zealand and North America, *E. abietinum* has been reported to be more damaging and responsible for wide-scale spruce mortality (Pillsbury, 1960; Zondag, 1983; Lynch, 2004).

E. abietinum has limited impact in the UK and Europe because populations of the aphid are reduced by periods of cold weather during the winter, and this prevents significant damage in most years (Carter, 1972; Powell and Parry, 1976; Day and Kidd, 1998). Global climate change however, is expected to increase mean winter temperatures in the UK by 1–2 °C by 2050 and to lead to a reduction in the number of days with frost (Hulme et al., 2002; Broadmeadow, 2005). If this increase in winter temperatures is realised, then overwinter survival of *E. abietinum* is likely to improve and spruce plantations will face an increased risk of defoliation (Evans et al., 2001). This is of particular significance for forestry in the UK, which has invested heavily in Sitka spruce, especially in upland areas in the north and west.

E. abietinum populations in the UK however, also appear to be strongly influenced by mortality caused by invertebrate natural enemies (Crute and Day, 1990; Day and Kidd, 1998; Day et al., 2006). High *E. abietinum* populations in one year are usually followed by low populations in the next year, and low populations are followed by rapidly increasing numbers, resulting in a strong and highly significant first order auto-correlation in population densities (Day and Crute, 1990; Zhou et al., 1997; Saldana et al., 2007; Westgarth-Smith et al., 2007). This intrinsic short-term population cycle often prevents *E. abietinum* populations increasing after a mild winter, and therefore outbreaks do not occur after every mild winter. Similar high–low population cycles occur in other tree-dwelling aphids (Dixon, 2005). In these species, the main factors driving the cycle appear to be intraspecific competition and a decline in host quality in the autumn after high populations in the spring (Dixon, 2005). In *E. abietinum* however, spring infestation does not lead to poorer host quality in the autumn (Williams et al., 2005), and the high–low population cycle appears to be driven primarily by a strong, but largely delayed and overcompensating response of predator and parasitoid populations to high aphid densities (Crute and Day, 1990; Day and Kidd, 1998).

Predicting the response of *E. abietinum* to climate change therefore requires an understanding of how populations of natural enemies might also respond to changes in climate and to changes in prey numbers. The same problem occurs in trying to predict how other herbivorous insects might respond to climate change (Harrington et al., 2001; Bale et al., 2002). *E. abietinum* is attacked by a wide range of generalist aphid-feeding predators, several species of parasitoids and entopathogenic fungi (Bejer-Peterson, 1962; von Scheller, 1963; Austarå et al., 1998; Nielsen et al., 2001; Day et al., 2006). The most important predators are coccinellid and cantharid beetles (Coleoptera: Coccinellidae & Canthariidae), brown lacewings (Neuroptera; Hemerobiidae) and the larvae of hoverflies (Diptera: Syrphidae). The species present in commercial spruce plantations have been listed in a number of studies (Austarå et al., 1997, 1998; Großner et al., 2005) and their impact on *E. abietinum* has been demonstrated by experiment (Leather and Owuor, 1996; Day et al., 2006) and by modelling (Crute and Day, 1990; Leather and Kidd, 1998). There is however, little information on how predator abundance varies spatially between and within forests, or in relation to aphid numbers. Consequently, it is difficult to assess the extent to which predators might respond to changes in environmental conditions or to potential increases in prey density.

One approach to predicting how insects might respond to climate change is to compare insect distribution and abundance along the climate gradient represented by different altitudes (Whittaker and Tribe, 1996, 1998; Fielding et al., 1999; Hódar and Zamora, 2004; Hodkinson, 2005). Population behaviour in the warmer climate at lower altitudes should give an indication of how populations are likely to behave at mid and higher altitudes in the future, and more generally as temperatures increase (Bale et al., 2002; Hodkinson, 2005). This is the approach used in the current study. Invertebrate predators of *E. abietinum* were sampled in commercial Sitka spruce plantations from 310 m to 610 m above sea-level and their abundance was related to local climate and aphid numbers, to assess the capacity for predators to respond to changes in environmental conditions and to changes in *E. abietinum* populations.

2. Materials and methods

2.1. Study site

The study was carried out in Radnor Forest in mid Wales (latitude 52°17′ N; longitude 3°11′ W) during 2001–2003. The forest is typical of the large commercial plantations of the west and north of the UK and covers 1390 ha, of which 65% is planted with Sitka spruce. Assessments of aphid density and continuous trapping of predators (sticky traps, flight interception traps, litterfall collectors) were carried out in six untreated experimental plots (0.05–0.08 ha in size) established as part of a wider study on the impact of *E. abietinum* on mid-rotation spruce (Straw et al., 2006). Five of these plots (Sites 1–5) were located on the same north-facing slope from 310 m (Site 1) to 610 m (Site 5) above sea-level (a.s.l.). The remaining plot (Site 6) was located at 460 m on a similar slope 1 km to the west. Aphid data were also available in 2001 from a further six study plots, located at the same altitudes, before these plots were treated with insecticide as part of the wider impact study.

All of the study plots were located in pure, unthinned stands of Sitka spruce, except at Site 1 where the stand contained 18% Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Fr.). The plots were positioned at least 30 m into the stand to reduce edge effects (Ozanne et al., 1997), and a permanent scaffold tower in the centre of each plot provided access to the canopy. Trees were 20–24-years old in 2001 and mean tree height varied from 8.3 m to 13.4 m (Straw et al., 2006). Climate data were obtained from three automatic weather stations (Delta-T Ltd., UK) positioned on top of the scaffold towers in the untreated plots at the lowest, mid and highest altitude sites (Table 1). These were maintained throughout the study period and provided hourly records of air temperature, rainfall and wind speed.

2.2. Population densities of *E. abietinum*

Population densities of *E. abietinum* were estimated by counting aphids and needles on shoots in the canopy. Counts were made by holding a small piece of plastic sheet against the underside of a shoot, and recording the number of aphids and needles visible through a 3 cm window cut in the centre of the sheet (Straw et al., 1998, 2006). Between 150 and 200 counts were made on each of two trees in the centre of each experimental plot (i.e. the two trees accessible from the scaffold tower) during the middle week of each month. Counts were made throughout the canopy and shoots were selected systematically from all age-classes of foliage and from different canopy positions (Straw et al., 2006).

In this study, variation in predator abundance was compared with peak *E. abietinum* densities, represented by the numbers of aphids on current and 1-year old shoots in May or June (where