

Direct and indirect effects of climate change on insect herbivores: Auchenorrhyncha (Homoptera)

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Abstract. 1. Novel manipulations of local climate were employed to investigate how warmer winters with either wetter or drier summers would affect the Auchenorrhyncha, a major component of the insect fauna of grasslands. Direct and indirect effects of climate manipulation were found.

2. Supplemented summer rainfall resulted in an increase in vegetation cover, leading to an increase in the abundance of the Auchenorrhyncha.

3. Summer drought, however, caused a decrease in vegetation cover, but this did not lead to a corresponding decrease in the abundance of the Auchenorrhyncha.

4. Egg hatch and the termination of nymphal hibernation occurred earlier in winter warmed plots; however, the rate of nymphal development was unaffected.

Key words. Auchenorrhyncha, climate change, insect herbivores, insect–plant interactions.

Introduction

The effects of host plant quality, predation/parasitism and abiotic factors on insect herbivore populations have been studied for many years (e.g. Dethier & MacArthur, 1964; Lawton, 1978; Price *et al.*, 1980; White, 1984), resulting in such interactions becoming a cornerstone of ecology. Recently, there has been a growing interest in how such interactions may be affected by a changing climate and other anthropogenic impacts on the natural environment. Although the responses of plants, as individuals, populations and simple assemblages, to climatic change have been the subject of recent attention (e.g. Woodward, 1992; Grime, 1997), the effects on their associated herbivores are far less well known.

The Auchenorrhyncha, including leaf, plant and frog hoppers, is a relatively well-known group of insect herbivores (e.g. Waloff, 1980), with knowledge of many species' ecology being greater than for many other groups of insects. The effects of host plant quality (e.g. Prestidge & McNeill, 1983), plant architecture (e.g. Brown *et al.*, 1992), plant species composition (e.g. Novotny, 1991) and successional age of the plant community (e.g. Hollier *et al.*, 1994) have all been shown to exert a major influence on auchenorrhynchan dynamics. Top-down effects have also been found to influence their dynamics (e.g. Whittaker, 1971, 1973; Waloff, 1980).

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Climate change scenarios, generated from General Circulation Models (GCMs) with a doubling of atmospheric CO₂, have predicted that the U.K. will probably experience a warming that will be most marked over winter (CCIRG, 1991; Houghton *et al.*, 1996). Additionally, there is likely to be an increase in anticyclonic behaviour during the summer, which may result in a 20% increase in precipitation (more thunderstorms) (CCIRG, 1991; Houghton *et al.*, 1996). However, there may also be long periods of drought between rain-bearing storms (CCIRG, 1991; Houghton *et al.*, 1996). A long-term manipulative field experiment was established in 1993 to address the question of how changes in local climate will affect the structure and functioning of calcareous grasslands. The effects of warmer winters, combined factorially with either wetter or drier summers, on the dynamics of the auchenorrhynchan community at a calcareous grassland site in the south of Britain are reported. The hopper populations, both in and adjacent to the current study site, have been studied previously (Whittaker, 1969; Brown *et al.*, 1992). These works provide valuable background information, not normally available in such studies.

Materials and methods

Site description

The experiment is located within a Jurassic corallian limestone grassland at Wytham Woods, Oxfordshire, U.K. The

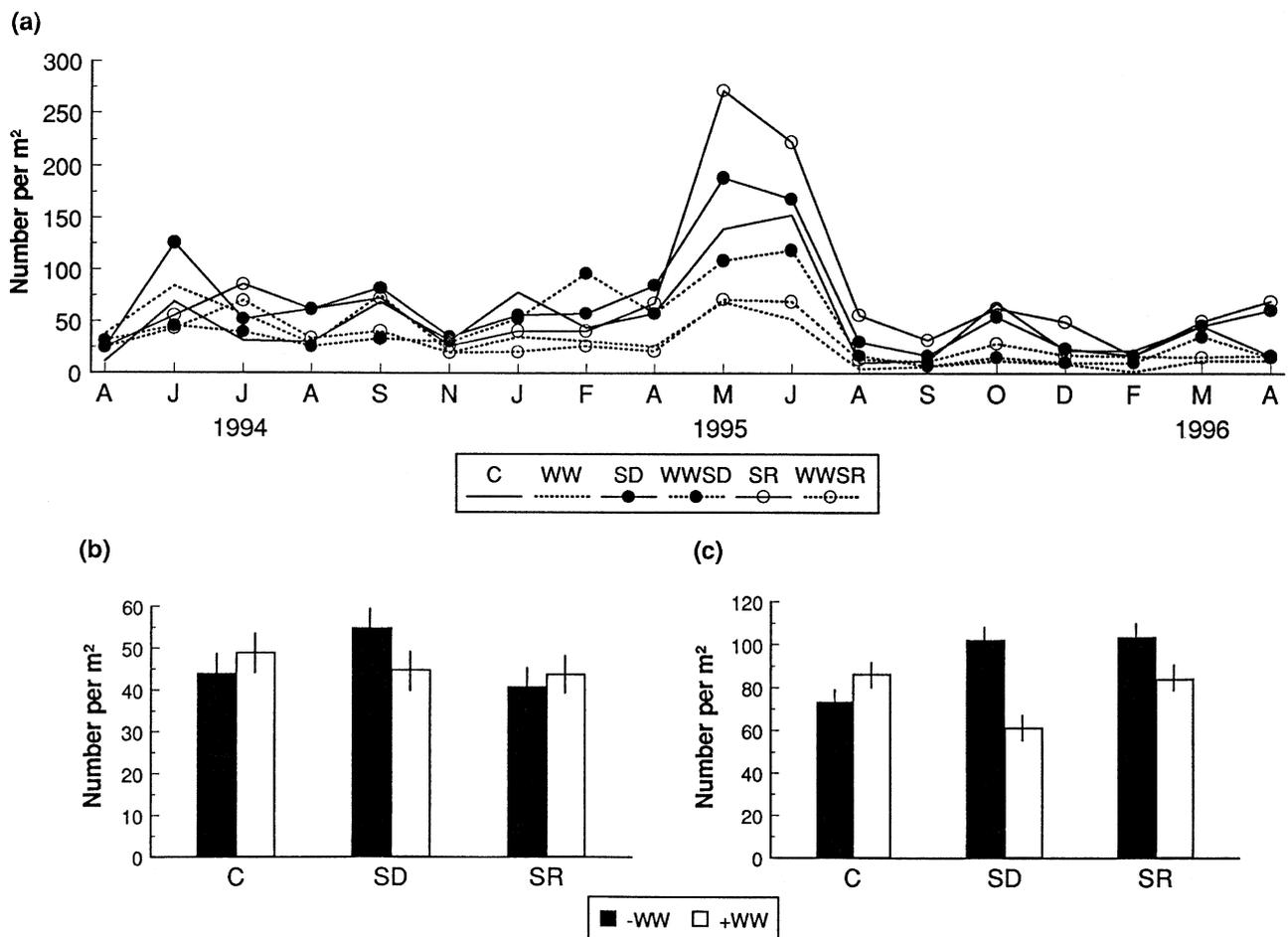


Fig. 1. Auchenorrhynchan dynamics under climate manipulations. (a) Two-year time course of total Auchenorrhyncha (nymphs + adults) to manipulation of local climate; C: control; WW: winter warming; SD: summer drought; SR: supplemented summer rainfall; (b) Pre-treatment densities of total Auchenorrhyncha in July 1993, and (c) Post-treatment densities of total Auchenorrhyncha (averaged across the 2-year time course). Bars represent ± 1 SE.

study site is situated within 1 ha of a 10 ha ex-arable field, in which cultivation ceased in 1982 (Gibson, 1986). The hectare has been fenced to exclude deer (the primary wild herbivore) and sheep (used for management of surrounding grassland). Pre-treatment vegetation sampling of the entire hectare took place at regular intervals during 1993, using point quadrat pins. A total of seventy-nine plant species was recorded; in terms of frequency of encounter, 63% were perennial grasses, 22% perennial forbs, 8% monocarpic perennial forbs, 3% annual forbs, 2% woody species and 2% mosses.

Experimental design

Field manipulations of local climate have been implemented to determine the potential impact of climate change on calcareous grassland structure and function. A randomized block design, with five replicates, was implemented to simulate the effects of warmer winters with either wetter or drier summers. Hence, there were six treatments per block: (1)

control (C: ambient climatic conditions); (2) winter warming (WW); (3) summer drought (SD); (4) supplemented summer rainfall (SR); (5) WW \times SD; and (6) WW \times SR. These manipulations were applied to 3 \times 3 m plots, separated by 2 m walkways. Treatments began in 1994 and the experiment is on-going. The long-term nature of the field experiment, its general aims and rationale, are given in Cummins *et al.* (1995).

Winter warming was applied through 1 kW heating cables at the soil surface. Cables were laid in rows 5 cm apart across a plot (after Hillier *et al.*, 1994). Temperature probes, connected to a Campbell's datalogger (CR 10; Campbell Scientific, Shepshed, Leicestershire, U.K.) that takes measurements every 30 s, were positioned randomly within the plots and maintained a 3 $^{\circ}$ C (± 0.1 $^{\circ}$ C) temperature differential from 1 November to 30 April the following year. Supplemented summer rainfall was applied from 1 June to 30 September each year. Supplementation of 20% over the 10-year average for the period was applied by spraying deionized water evenly across relevant plots weekly. A complete summer drought was imposed from 1 July to 31 August each year by mobile non-invasive

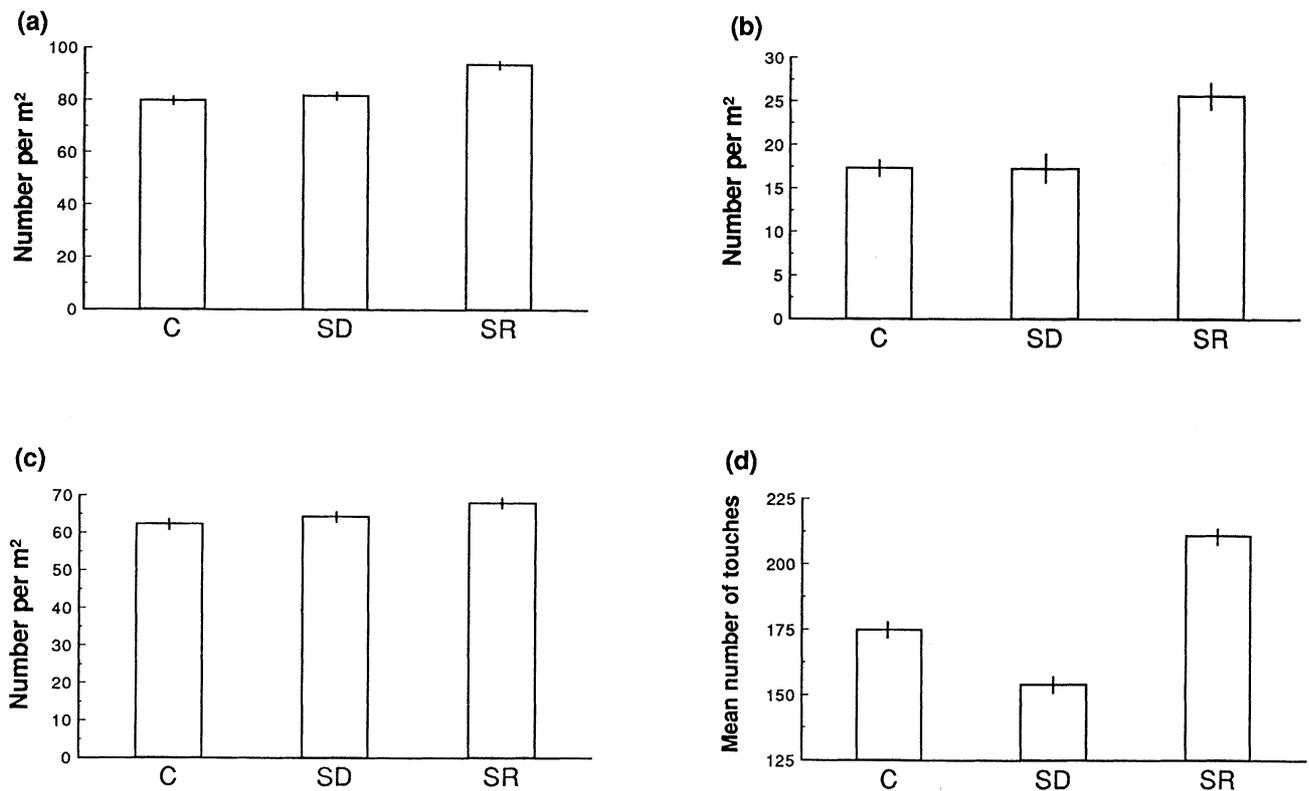


Fig. 2. Main effects of summer drought and supplemented summer rainfall on Auchenorrhyncha. (a) Total; (b) Adults; (c) Nymphs, and (d) Vegetation cover expressed as the number of touches of point quadrat pins. C: ambient summer rainfall conditions; SD: plots exposed to summer drought; SR: plots exposed to supplemented summer rainfall. Bars represent ± 1 SE.

rain shelters. Each shelter was a 3×3 m polycarbonate structure (scaled up from a design by Buckland, 1994) that moves across the relevant droughted plot when activated by a rain sensor. Shelters remain parked adjacent to the treated plots when there is no rainfall.

Sampling

Auchenorrhyncha were sampled using a Vortis suction sampler (Burkhard Manufacturing, Rickmansworth, Hertfordshire, U.K.) at 6-weekly intervals from April 1994 to April 1996, giving a total of eighteen samples. The insects, collected from six randomly positioned sucks within each 3×3 m plot, were pooled to give a plot sample, in which 1.3% of the total area was sampled at any one time. Similar suction sampling within neighbouring field experiments had no significant effects on the insect populations (Brown *et al.*, 1992). All individuals were counted and stored in 70% alcohol for identification (nomenclature follows Le Quesne & Payne, 1981). All adults and, where possible, nymphs were identified to species; additionally, the nymphs of the most common species, *Euscelis incisus* (Kirschbaum), were aged to instar. The abundance and age structure of nymphal *Philaenus spumarius* (L.), feeding on *Pastinaca sativa* L., were assessed from direct counts from their protective spittle within the

3×3 m plots. The number of nymphs found in 0.5 man hours was counted and identified to instar (by J.B.W.) on four different sample dates in 1996 (23 April, 23 May, 5 June and 22 June). Live individuals were carefully returned to their spittles immediately after ageing, a procedure that has been found to have no effect on the subsequent performance and survival of these spittlebugs (J. B. Whittaker, unpublished data). Vegetation was sampled by point quadrat pins at the same intervals, using fifty pins per treatment plot (*sensu* Brown & Gange, 1989), to give information on plant species richness, frequency of encounter, architecture and cover (cover abundance).

Statistical analysis

ANCOVA was used to analyse the randomized block design with three levels of summer watering (C, ambient rainfall; SD, droughted plots; SR, supplemented plots) and two levels of winter warming (+ WW, warmed plots; - WW, unwarmed plots) (Snedecor & Cochran, 1989). This tested for auchenorrhynchan responses to the treatments with respect to those of their host plants. Auchenorrhynchan numbers were square-root transformed before being analysed with a normal error structure (Sokal & Rohlf, 1995). The analysis was conducted on every sampling date and a repeated measures

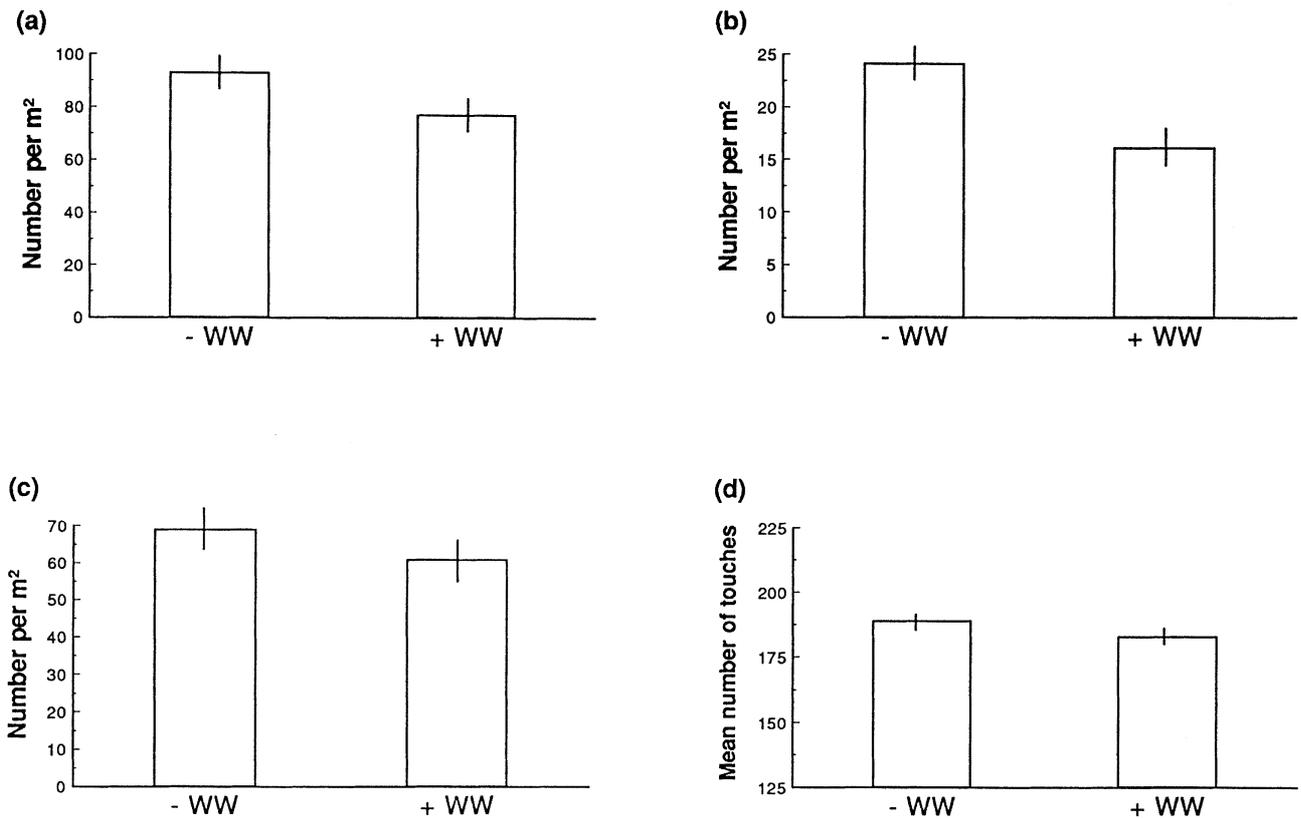


Fig. 3. Main effects of winter warming on Auchenorrhyncha. (a) Total; (b) Adults; (c) Nymphs, and (d) Vegetation cover expressed as the number of touches of point quadrat pins. -WW: ambient winter temperatures; + WW: plots exposed to winter warming. Bars represent ± 1 SE.

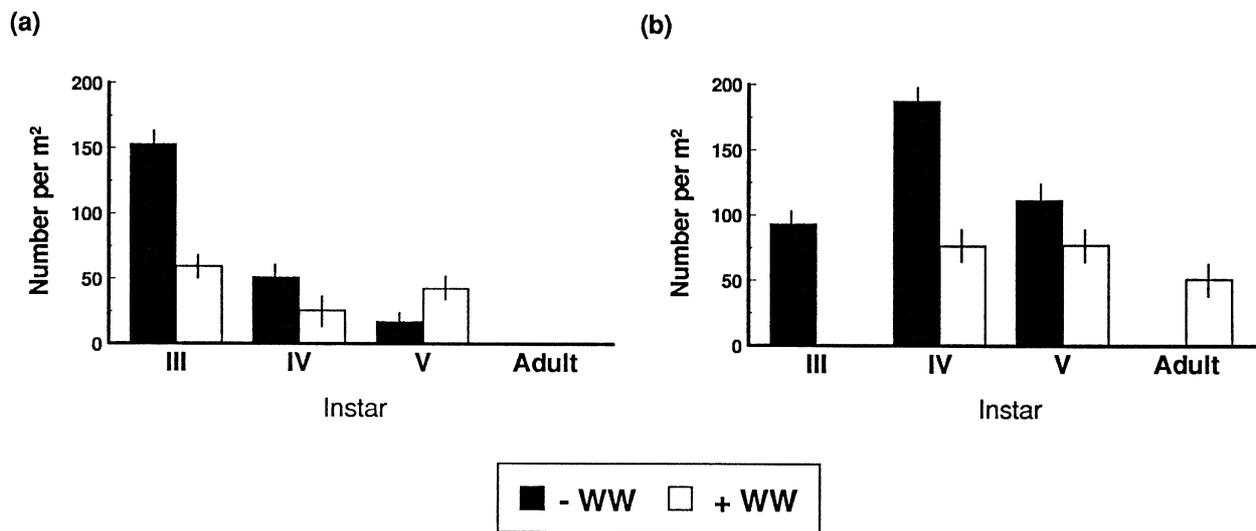


Fig. 4. The main effects of winter warming on the age structure of *Euscelis incisus* nymphs. (a) 14 February 1996 and (b) 19 March 1996. -WW: ambient winter temperatures; + WW: all plots exposed to winter warming. Bars represent ± 1 SE.

analysis was used to determine whether the treatments were having a long-term impact (repeated measures main effect) or whether the effects were more transient (repeated measures treatment × date interactions). Correlations between

auchenorrhynchan density and plant attributes suggested a strong association with plant cover, whereas plant frequency, species richness and architecture were less closely related. Hence, cover abundance was used as the covariate. If the

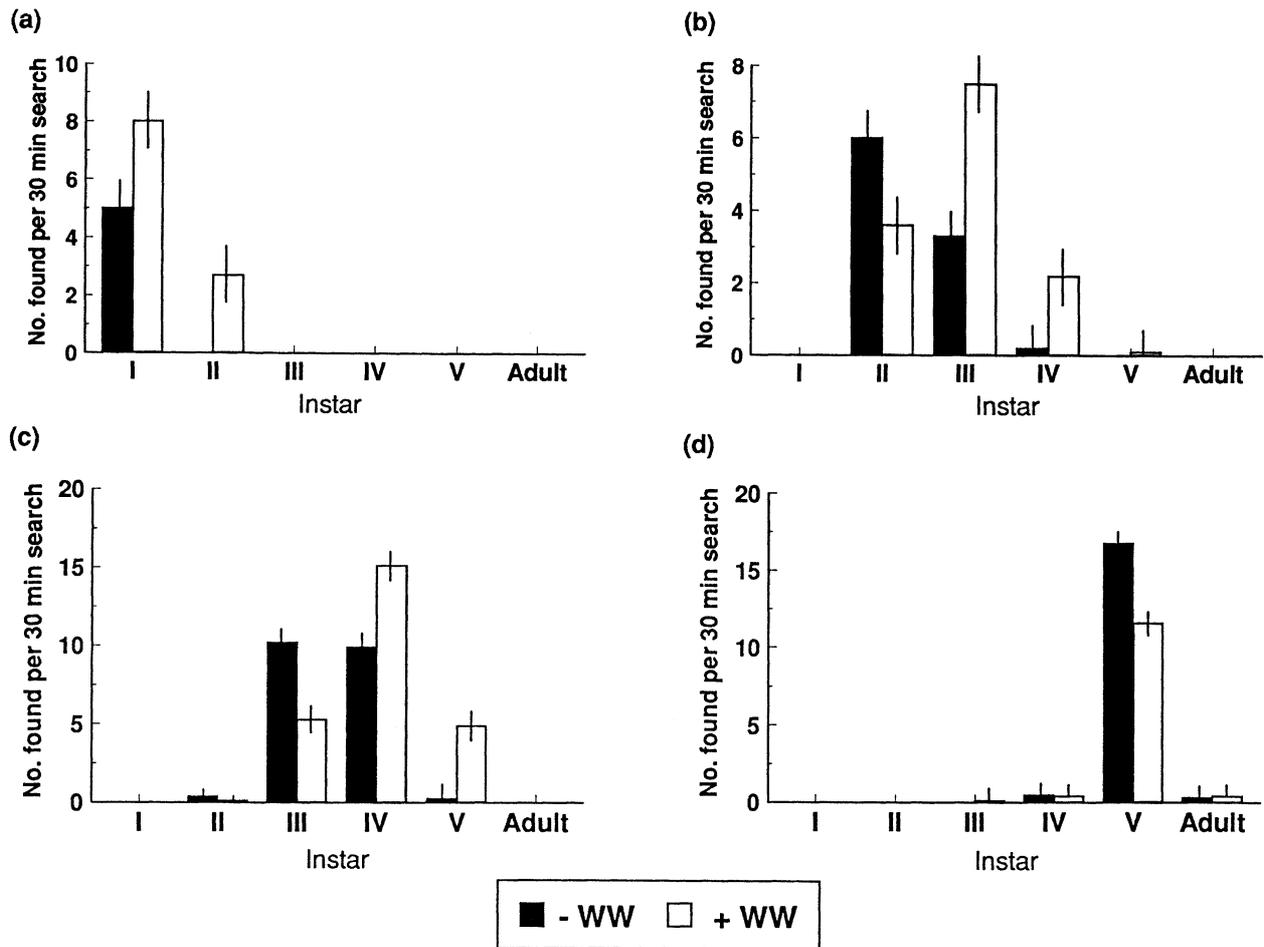


Fig. 5. The main effects of winter warming on the age structure of *Philaenus spumarius* nymphs. (a) 23 April 1996; (b) 23 May 1996; (c) 5 June 1996, and (d) 22 June 1996. -WW: ambient winter temperatures; + WW: plots exposed to winter warming. Bars represent ± 1 SE.

ANCOVA was not significant, it indicated that the auchenorrhynchan response was correlated with the change in the vegetation (i.e. increasing or decreasing in density in proportion to vegetation cover). However, if the ANCOVA was significant, the auchenorrhynchan response was not correlated with the response of the vegetation to the climate manipulation, and may therefore represent a direct effect of the manipulations on the growth rate or mortality of the hopper. Intuitively, the Auchenorrhyncha would be expected to respond closely to changes within their host plant, and the results of the ANCOVA would therefore be expected to show no statistical significance.

The number of nymphs of each instar of *Euscelis incisus* and *Philaenus spumarius* for each date was analysed using GLIM 3.77 (Baker, 1987), using an analysis of deviance with a Poisson error structure and a deletion of factors to the minimum adequate model. Hence, significance is determined by χ^2 comparisons (Crawley, 1993). In addition, an index of development for *Philaenus spumarius* was calculated for each sample date using the equation;

$$I = \sum_{i=1}^5 (n_i \times i) / T$$

(after Hodkinson *et al.*, 1979), where: I = the index of development; i = instar age; n_i = number of individuals of instar i; and T = total number of individuals found.

Results

A total of thirty-one species was recorded between July 1993 and May 1996. This is \approx 50% of the species found by Brown *et al.* (1992) and 30% of the total species list for all habitats in Wytham Woods recorded by Whittaker (1969). In midsummer 1993, the two most common species were *Elymana sulphurella* (Zetterstedt) and *Zyginidia scutellaris* (Herrich-Schaeffer) (28% and 36% of the community, respectively), whereas at the end of 2 years of treatments, *Euscelis incisus* and *Agallia ribauti* (Ossiannilsson) were the most abundant (21% and 27% of the community, respectively). Interestingly, these species have reduced wings, which clearly limits their ability to disperse. Indeed, there was little movement between the plots within the experimental blocks in response to the climate manipulations, a trend confirmed by mark and recapture experiments (Harold *et al.*, 1996).

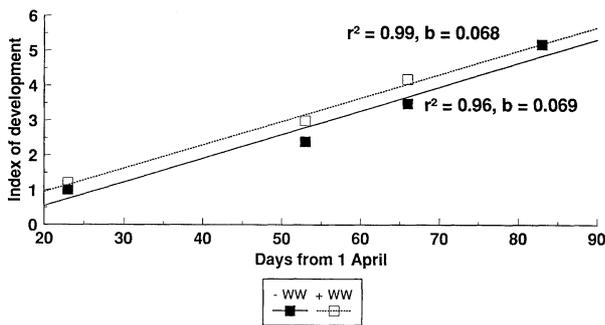


Fig. 6. The main effects of winter warming on the development index of *Philænus spumarius*. The slope of the regression lines (b) represents the rate of development. -WW: ambient winter temperatures; +WW: plots exposed to winter warming.

It is the main effects from the repeated measures ANCOVA that are reported primarily, as treatment \times date interactions may be subject to a variety of interpretations. Where these are reported, such interactions are interpreted as an indication that the treatments are not having consistent effects through time. Single date analyses are used to support the results from the repeated measures analysis.

The dynamics of the total auchenorrhynchan fauna, as displayed by suction sampling, over the 2 year time course are illustrated in Fig. 1a. There were no significant differences between the treatments during pre-treatment samples (Fig. 1b). However, when the treatments were considered throughout the whole experimental period, trends were apparent (Fig. 1c).

There were significant main effects (irrespective of temporal effects) of the summer watering regimens ($F_{2,23} = 12.15$, $P < 0.001$; Fig. 2a), with numbers being maintained in droughted plots, even though the vegetation cover was decreased compared to the control (Fig. 2d). Supplemented summer rainfall resulted in an increase in hopper density, as predicted from the response of the vegetation, which showed an increase compared to the control. In this case, the ANCOVA was not significant. The adults and nymphs, when considered separately, responded in a similar way, with numbers not significantly reduced by drought ($F_{2,23} = 4.76$, $P < 0.05$; Fig. 2b and $F_{2,23} = 11.53$, $P < 0.001$; Fig. 2c, respectively) and increased by supplemented summer rainfall. This trend was also seen in the two dominant species, *E. incisus* and *A. ribauti*.

No significant main effects of winter warming, or interactions between the treatments for total Auchenorrhyncha (Fig. 3) were found, a trend mirrored by the nymphs (Fig. 3c) and the vegetation (Fig. 3d). However, numbers of adults were significantly decreased in warmed plots ($F_{1,23} = 11.83$, $P < 0.01$; Fig. 3b).

The age structure of *E. incisus* nymphs was also affected by winter warming (main effect) (Fig. 4). There were significantly fewer third-instar nymphs ($\chi^2_1 = 5.01$, $P < 0.05$) and significantly more fifth-instar nymphs ($\chi^2_1 = 4.01$, $P < 0.05$) in winter warmed plots on the first sample date (Fig. 4a). This trend was also seen at the second sample date (6 weeks later)

when there were no third instars, significantly fewer fourth instars ($\chi^2_1 = 5.6$, $P < 0.05$) and reduced numbers of fifth instars (but not significant), recorded from winter warmed plots (Fig. 4b). Indeed, adults were only recorded from warmed plots on this date (Fig. 4b).

Similarly, the age structure of *P. spumarius* was affected by winter warming (Fig. 5). On the first sample date, there was a trend for more first-instar nymphs in warmed plots ($\chi^2_1 = 3.21$, $P > 0.05$), whereas second-instar nymphs were only found in warmed plots (Fig. 5a). By the second date, there were significantly fewer second-instar nymphs ($\chi^2_1 = 8.6$, $P < 0.01$), but significantly more third and fourth instars ($\chi^2_1 = 25.99$, $P < 0.001$ and $\chi^2_1 = 29.25$, $P < 0.001$) in winter warmed plots (Fig. 5b). This skewed age structure was also seen on the third sample date, with significantly fewer third-instar nymphs ($\chi^2_1 = 7.46$, $P < 0.01$), but significantly more fourth and fifth instars ($\chi^2_1 = 6.46$, $P < 0.01$ and $\chi^2_1 = 76.6$, $P < 0.001$) in winter warmed plots (Fig. 5c). By the final sample, when most of the instars were fifths, fewer were recorded in winter warmed plots ($\chi^2_1 = 14.36$, $P < 0.001$; Fig. 5d), although there was no corresponding increase in number of teneral adults in this treatment.

Interestingly, winter warming had no effect on the rate of development, as the slopes of the regression lines were identical (b = 0.068, warmed and b = 0.069, ambient; Fig. 6).

Discussion

Generally, the auchenorrhynchan dynamics were as expected from previous work at Wytham (Whittaker, 1969; Brown *et al.*, 1992) and displayed a range of responses to the climate manipulations. Supplemented summer rainfall led to a large increase in the number of Auchenorrhyncha (nymphs and adults) (Fig. 2), which was directly related to the increase in vegetation cover (Fig. 2d), particularly that of grasses. This was to be expected, as Kontkanen (1950), in an early study of the leafhoppers of Finnish meadows, suggested that moisture content of the habitat may be a key feature in determining the relative abundance and community composition of leafhoppers. Under summer drought, the cover of vegetation was decreased significantly (Fig. 2d) and thus auchenorrhynchan numbers would be expected to decline. However, numbers were maintained or increased in this treatment (Fig. 2), suggesting the importance of other interactions. The Auchenorrhyncha are known to respond to the nutritional quality of food plants. Prestidge & McNeill (1983) have shown that leafhopper populations feeding on the grasses *Holcus lanatus* L. and *H. mollis* L. respond readily to nitrogen fluctuations within the host plant, and that increased levels of N induce a higher abundance of leafhoppers. Drought stress is known to lead to changes in the levels of soluble nitrogen and carbohydrate in the foliage (Hsiao, 1973; Mattson & Haack, 1987), resulting in foliage of higher quality and consequently improved insect performance (White, 1984; Mattson & Haack, 1987; Holtzer *et al.*, 1988; Masters *et al.*, 1993; Masters, 1995). This could well explain the response of the Auchenorrhyncha to summer drought.

Under climate change, the winters in the U.K. are likely to be warmer (CCIRG, 1991), and this may have direct and indirect effects on the population dynamics of the Auchenorrhyncha. Indeed, fewer adults were recorded from warmed plots, particularly in the spring and summer periods (Figs 1 and 3). This may be due to differential mortality of overwintering adults or nymphs or decreased overwintering egg viability. However, nymphal populations were not affected by winter warming (Fig. 3c), and, thus, differential nymphal mortality seems an unlikely cause of the lower populations of adults. Winter warming may also be affecting overwintering Auchenorrhyncha by causing a change in egg hatch date and/or nymphal development rates as a direct effect on the insect's physiology. By maturing earlier in warmed plots, young adults would be at a greater risk from extreme events, e.g. late cold spells, leading to a reduction in adult numbers. A change in developmental phenology would result in nymphs recorded from warmed plots being older than those recorded from ambient conditions, as found in *E. incisus* and *P. spumarius*. *Euscelis incisus* was the commonest species recorded and gave the only reliable age data from suction samples. *Philaenus spumarius* is relatively easy to locate (spittle on the stems or under leaves) and can be aged *in situ*, so the population can be monitored throughout its development. The age structure of both species clearly showed that individuals recorded from warmed plots were significantly older than those recorded from unwarmed plots (Figs 4 and 5). Thus, the egg diapause of *P. spumarius*, or the nymphal hibernation of *E. incisus*, may be broken earlier by milder winters, and/or the following nymphs may develop faster (i.e. a direct effect of temperature on insect development rates; *sensu* Uvarov, 1931). An entire population of *P. spumarius* was followed accurately throughout development, and the development rates of nymphs of *P. spumarius* were calculated and plotted (Fig. 6). There was no difference between warmed and ambient plots. However, the difference in the intercept indicates that there is a different egg hatch date, with eggs in warmed plots hatching up to 6 days earlier.

Climate change will affect host plant physiology, growth, species assemblages and successional processes, and these all have an impact on plant–insect relationships. Due to the complexity of indirect interactions between climate, vegetation and insect herbivores, prediction is difficult, but for the Auchenorrhyncha there is evidence that they will have larger populations, irrespective of the response of the vegetation, although the effects of predators and parasitoids will need consideration. Indeed, droughting events may lead to an increased number of insects of potential economic significance in agricultural systems (Cammell & Knight, 1992). Furthermore, the direct effect of climate on insects may lead to phenological shifts between herbivore and host and parasitoid/predator and host. The effect of milder winters on the age structure of the Auchenorrhyncha suggests that these insects will mature earlier, thus shifting the life cycle's seasonality and potentially, for bivoltine or multivoltine species at least, providing the possibility of further generations within a season.

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