REVIEW

Herbivory in global climate change research: direct effects of rising temperature on insect herbivores

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Abstract

This review examines the direct effects of climate change on insect herbivores. Temperature is identified as the dominant abiotic factor directly affecting herbivorous insects. There is little evidence of any direct effects of CO_2 or UVB. Direct impacts of precipitation have been largely neglected in current research on climate change. Temperature directly affects development, survival, range and abundance. Species with a large geographical range will tend to be less affected. The main effect of temperature in temperate regions is to influence winter survival; at more northerly latitudes, higher temperatures extend the summer season, increasing the available thermal budget for growth and reproduction. Photoperiod is the dominant cue for the seasonal synchrony of temperate insects, but their thermal requirements may differ at different times of year. Interactions between photoperiod and temperature determine phenology; the two factors do not necessarily operate in tandem. Insect herbivores show a number of distinct life-history strategies to exploit plants with different growth forms and strategies, which will be differentially affected by climate warming. There are still many challenges facing biologists in predicting and monitoring the impacts of climate change. Future

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research needs to consider insect herbivore phenotypic and genotypic flexibility, their responses to global change parameters operating in concert, and awareness that some patterns may only become apparent in the longer term.

Introduction

Climate change is occurring (Houghton *et al.* 1996, 2001). During the past 100 years global-average surface temperatures have increased by approximately 0.6 °C (the largest increase of any century during the past 1000 years), with the 1990s the warmest decade and 1998 the warmest year since instrumental records began (Houghton *et al.* 2001). The Third IPCC report predicts that global-average surface temperature will increase further by 1.4–5.8 °C by 2100 with atmospheric carbon dioxide (CO_2) concentrations expected to rise to between 540 and 970 p.p.m. over the same period. It is predicted that the British Isles will experience temperature and CO_2 elevations of this magnitude (CCIRG 1991, 1996; Hulme & Jenkins 1998; Houghton *et al.* 2001). Precipitation, ultra-violet B (UVB) penetration and extreme events (e.g. flooding, storminess and drought) are also predicted to increase, but there is less certainty about the magnitude of these changes. The consequence of such changes for natural ecosystems presents a major challenge for biologists. A clearer understanding of how a changing climate affects species, populations, communities and ecosystems, and of the mechanisms involved, will enable better prediction of its overall impact. Models of climate change impacts frequently fail to consider these effects; for example, the effects of herbivores, central to ecosystem structure and function (e.g. Crawley 1983; Mulder *et al.* 1999), are often either treated as constant (i.e. a black box), included as a disturbance factor, or ignored (e.g. Adams & Woodward 1992).

In 1998 the Natural Environment Research Council's (NERC) Terrestrial Initiative in Global Environmental Research (TIGER) programme (Cummins *et al.* 1995; Cummins & Watkinson 1999) organized a synthesis workshop to consider the consequences of climate change for herbivores. Insects were taken as a focus, reflecting both the proportion of research effort within the TIGER programme and the participants' own particular expertise. Examples were drawn predominately from the British Isles, reflecting a concentration of work in this geographical locality, although other regions were also considered. Effects of climate change on insect herbivores can be direct, through impacts on their physiology and behaviour, or indirect, where the insects respond to climate-induced changes mediated through other factors, notably the host plant.

In this review we consider the direct effects of climate change on insect herbivores, but we concentrate on the effects of temperature. There is limited experimental evidence for the direct effects of CO_2 on insects (e.g. Agrell *et al.* 2000; Stange *et al.* 1993; Caulfield & Bunce 1994; Stange 1997) and the even more limited number of studies on the consequences of changing UVB levels on insect herbivores give conflicting results (see Hatcher & Paul 1994; McCloud & Berenbaum 1994). Little is also published about the direct effects of changing precipitation patterns on insects, although much can be surmised, particularly of rainfall as an enhanced mortality factor (e.g. Thacker *et al.* 1997; Dixon 1998). Existing studies suggest that direct effects of temperature are likely to be larger and more important than any other factor. Direct effects of temperature rise on insects may be greater in the polar regions than in temperate or tropical zones, reflecting the more severe environmental conditions, the tighter constraints and the prediction of much larger proportional temperature rises in these areas (Bale *et al.* 1997; Convey & Block 1996; Hodkinson *et al.* 1998; Vernon *et al.* 1998).

The aim of this review is to explore the direct impacts of temperature elevation, as a principal driver of climate change, on insect phenology, life cycles and distribution (including movement and migration) before considering the physiological and ecological mechanisms involved and the implications for overwintering. Natural, rather than agricultural (see Cammell & Knight 1992; Cannon 1998), systems will be the main focus of this review as they include an existing template of spatial and phenological variation in the environment to which insect herbivores respond.

Life cycles, phenology and distribution

For insect herbivores, the ability to complete their life cycle represents a successful adaptation to both their host plant and to the climatic environment in which they are found. Climate can act directly on an insect either as a mortality factor or by determining the rate of growth and development. Using our knowledge of the effects of

elevated temperature on insect herbivores and our understanding of insect and plant life-history strategies, we can generate hypotheses on how insect life-history characteristics and distributions may respond to predicted climate change scenarios.

Life-history strategies

Insect herbivores generally employ one of six life-history strategies:

1 Take as long as is necessary (Methuselah): the life cycle may run over several years with growth and development dependent on climatic conditions. There is loose association with the host plant and its phenology. Example: Arctic moths (*Gynaephora* sp.) may take up to 14 years to complete their life cycle (Kukal & Kevan 1987).

2 Stop-go: insect herbivore growth and development is controlled by environmental cues, starting and stopping in synchrony with seasonal changes. The life cycle can go through more than one stop-go cycle but each time the cycle length is synchronized and of a fixed duration. Example: the psyllid *Strophingia ericae* which has a 2-year life cycle (Hodkinson 1973; Miles *et al*. 1998).

3 Grab it while you can: the host plant is only available as a food resource for a limited interval within a growing season. Close synchrony of the insect life cycle with plant phenology is vital and usually there is only a single generation per year. The seasonal cycle may be linked to moisture availability (Mediterranean/seasonal tropical zones) or temperature (temperate/boreal zone). Example: willow (*Salix*) psyllids *Cacopsylla* sp. (Hodkinson & White 1979) and many univoltine British butterflies (Dennis 1993).

4 Keep on trying while you can: the host plant remains suitable for continuous development throughout a limited growing period, allowing two or more insect generations per season. Rates of development vary within season, depending on temperature and host plant condition. Example: the butterfly *Aglais urticae* on *Urtica dioica* (Bryant *et al*. 1997) and autoecious aphids such as *Drepanosiphon platanoidis* on *Acer pseudoplatanus* and *Aphis rumicis* on *Rumex* sp. (Dixon 1998).

5 When in doubt hop about: as one host plant becomes 'unsuitable' the insect moves on to a neighbouring plant. In temperate regions, this category includes oligophagous and polyphagous insects that can exploit a seasonal progression of different host plant species (e.g. frit fly *Oscinella frit* on Gramineae and the butterfly *Pieris napi* on Cruciferae) and heteroecious aphids that switch between host plants (Dixon 1998). In seasonal tropical forests, this category includes new-shoot feeding species that switch between individual trees of the same species when flushing cycles are asynchronous and sporadic (e.g. the psyllids *Leuronta trichiliae* on *Trichilia cipo* and *Euceropsylla* species on *Inga* sp. in Panama) (Brown & Hodkinson 1988).

6 Never give up: development is continuous on a single host in a non-seasonal environment, with several generations per year. Example: many, but not all, moist tropical forest herbivorous insects. A further variation on this theme in seasonal environments are species that may be adapted to pass through unfavourable periods in any one of the egg, larval, pupal (endopterygotes) or adult stage. In these cases the life cycle also usually includes a seasonal synchronization mechanism such as diapause or photoperiodic inhibition of development (Hill & Hodkinson 1996; Gomi 1997; Miles *et al*. 1998).

Life-history strategy responses to temperature

Temperature may induce changes in life-cycle duration (rate of development), voltinism, population density, size, genetic composition, extent of host plant exploitation as well as local and geographical distribution linked to colonization and extinction. These effects are likely to be greatest in above-ground herbivores, exposed to the full variability of micro- and macroclimate, while soil-dwelling species experience thermal regimes that are buffered by the denser soil environment. Many species are limited in their distribution by summer heat availability rather than the lethal effect of extreme temperatures. Examples include the Arctic aphid *Acyrthosiphon svalbardicum* on *Dryas octopetala* (Strathdee *et al*. 1993), the spittle bug *Neophilaenus lineatus* along an altitudinal temperature gradient in Scotland (Whittaker & Tribe 1996), the psyllids, *Cacopsylla palmeni, C. brunneipennis* and *C. palmeni* on *Salix lapponum* in Norway (Hill & Hodkinson 1995), the British *Strophingia* sp. on *Calluna* sp. and *Erica* sp. (Miles *et al*. 1997; Hodkinson *et al*. 1999) and many British butterflies (Dennis 1993).

Effects of temperature on relative growth rates and phenological synchrony of insects and plants. Plant growth form and seasonal availability strongly influence the life-history strategy of insects associated with them (Table 1). Successful life-cycle completion in many host-specific insect herbivores requires close synchrony with host phenology. The plant may, for example, only be available for insect development for a relatively short time period during its growth stage. As climate becomes less favourable for insect development, synchrony becomes a more critical feature and particular insects become progressively less successful at completing their life cycle on specific host plants. The limited plant availability restricts any possibility of increased voltinism of the insect (e.g. the 'grab it' strategy, Table 2). For

Table 1 Insect/plant life-history strategy matrix indicating which insect types are most likely to be found on a range of plant types. Relative apparency of plant types are given on a scale of 1 (low) to 4 (high). The relative exposure times, of the plant to the insect, within one generation also are compared on a scale of 1 (low) to 4 (high). Plant growth strategies are based on Raunkiaer's (1934) classification: therophytes, bud position as seed (T); geophytes, bud position below ground (G); hemicryptophytes, bud position at the soil surface (H); chamaephytes, bud position < 0.25 m above the soil (C); and phanaerophytes, bud position > 0.25 m above the soil (P). d, deciduous vegetation; e, evergreen vegetation. The matrix is limited by data availability; *, data currently available from temperature manipulation experiments

	Plant strategy							
	T	G	H	C (d)	C (e)	P (d)	P (e)	Relative exposure time
Apparency (above ground)	1	2	2	3	4	3	4	
Apparency (below ground)	1	4	4	4	4	4	4	
Insect strategy (above ground)								
Methuselah	✓	✓	✓	✓	✓			4
Stop-go				✓	✓*	✓	✓	3
Grab it		✓	✓*	✓*	✓	✓*	✓	1
Keep trying		✓	✓*	✓	✓	✓	✓*	2
Hop about	✓*	✓*	✓*	✓*		✓*		2
Never give up					✓		✓	1

example, the psyllid *Cacopsylla groenlandica* feeds on shoots and catkins of four willow (*Salix*) species in southern Greenland but at the northern limit of its range is restricted to feeding on catkins of one willow (*Salix*) species, despite the presence of alternative hosts (Hodkinson 1997). Temperature, acting on differential growth rates of an insect and it's host plant, might set the upper and lower limits of an insect's distribution range (MacLean 1983; Fig. 1). At higher latitudes (more northern or southern climes) where temperature is lower, the host plant grows too slowly to support insect development while in warmer areas (mid–low latitudes), the plant may develop too quickly. Only over the mid part of the range are the insect herbivore and host plant's phenology in synchrony (Fig. 1).

Changes in host plant exploitation linked to temperature and phenology. Host plant and insect herbivore synchrony may also limit both the possible range of host plant species exploited and the actual plant tissues utilized. The psyllid *C. groenlandica* expands its range of willow (*Salix*) host-plant species from one to four along a latitudinal gradient as the demands of temporal synchrony lessen as the thermal environment becomes more benign (Hodkinson 1997). Similarly, *C. groenlandica* in Greenland and *C. propinqua* in alpine Norway change from feeding solely on catkins to feeding on both catkins and leaf tissues as the demands of phenological synchronization lessen along latitudinal and altitudinal gradients, respectively (Hodkinson 1997; Hill *et al*. 1998).

Tight phenological synchrony is often required for certain herbivore species to perform well on a host plant (Feeny 1970). Under climate change scenarios there is likely to be increased asynchrony between host plant and insect herbivore, with obvious adverse consequences (Dewer & Watt 1992). However, for some species, e.g. *Operophtera brumata* on oak (Buse & Good 1996), Sitka spruce (Watt & McFarlane 1991) and heather (Kerslake & Hartley 1997), tight phenological synchrony does not appear to be essential. Thus, in these cases, the impact of climate change remains particularly unclear.

Predicting life-history responses to temperature

Data to assess the direct impact of temperature on the life cycle, population dynamics and distribution of herbivorous insects originate from many sources. These range from simple temperature manipulation experiments at one or more localities (e.g. Strathdee *et al*. 1993, 1995; Strathdee & Bale 1995), the use of altitudinal/latitudinal gradients as spatial analogues for climate change (summarized by Hodkinson & Bird 1998), studies of insect/host plant synchrony (e.g. Hunter 1992; Quiring 1994; Aizen & Patterson 1995; Hill & Hodkinson 1995; van Dongen *et al*. 1997), correlation studies between distribution patterns and climatic variables (e.g. Bryant *et al*. 1997; Judd & Hodkinson 1998; Hodkinson *et al*. 1999), to the development of climatic models for pest forecasting (e.g. Porter *et al*. 1991; Fleming & Volney 1995; Williams & Liebhold 1995).

Table 2 Insect/plant life-history strategy matrix (as in Table 1) showing predictions for changes in insect voltinism (generations per unit time) with increased summer temperatures. Increases are denoted by +, no change by 0. All insect strategies are predicted to have an increased number of generations per year, apart from particularly the 'Grab it' strategy and possibly the 'Stop-go' strategy. There is a necessary close synchrony (because of limited host-plant availability) between insect and host plant, restricting the possibility of increased voltinism for insects with the 'Grab it' strategy. 'Stop-go' insects are less dependent upon host-plant availability in time (they live on their hosts) but have growth and development synchronized with the seasons. Hence, if increased temperature leads to an increased length of favourable seasons, then there is the possibility for an increase in voltinism. See text for details of the respective strategies

				C (d)	C (e)	P (d)	P (e)
	T	G	H				
Insect strategy							
Methuselah	+	+	+	+	+		
Stop-go				0+	0+	0+	0+
Grab it		0	0	0	0	0	0
Keep trying		+	+	+	+	+	+
Hop about	+	+	+	+		+	
Never give up					+		+

(Plant strategy)

The responses of insect life-histories to climate change are likely to be both complex and varied, depending, as previously considered, on the type of insect life-history and the growth strategy of the host plant (Table 1). Latitude and altitude can have marked impacts on insect life-history and frequently utilize the phenotypic flexibility and genotypic adaptability of many species (e.g. Kerslake *et al*. 1996). However, we can begin to predict the likely response in each of our listed insect life-history parameters to particular climate change scenarios. Predictions can be assembled in the form of a matrix for all possible insect/plant type combinations. The matrices then become working hypotheses. A single example of this approach is given in Table 2, where knowing the insect and plant life-history strategies enables simple predictions of whether the insect will increase, decrease or show no change in the population/ distribution parameter recorded, e.g. voltinism, in response to increasing temperature. From these matrices predictions can be made about insect responses to rising temperature, as shown in Table 2. Testing these hypotheses is dependent on available data and, as shown in Table 1, data for temperature related responses is only available for approximately 50% of the possible matrix cells. This synoptic approach must, however, be linked to
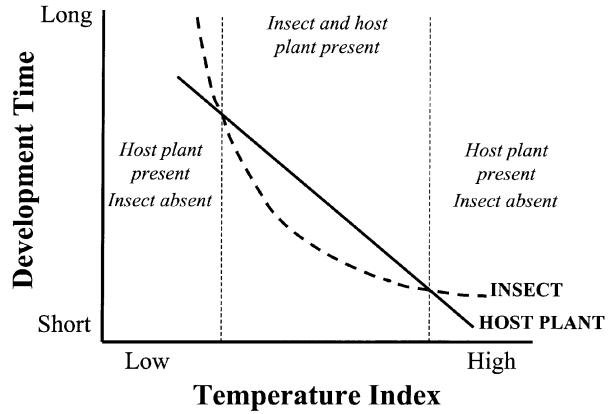

Fig. 1 Model showing how the relative development rates (time) of an insect and its host plant at different temperatures might set the distribution limits of host-specific insect herbivore species (after MacLean 1983). In the northern part of the range (low temperature index), the host plant grows too slowly to support insect development, whereas in the south (high temperature index), the plant develops too quickly. Only over the mid-part of the range is the insect herbivore able to match its phenology to that of its host plant.

a more detailed consideration of the physiological processes considered in the next section.

Insect development, voltinism and distribution

The number of insect species per unit area tends to decrease with increasing latitude (Gaston & Williams 1996; Wilf & Labandeira 1999). A similar trend is usually found with increasing altitude (Gaston & Williams 1996). Climatic warming will allow the majority of temperate insect species to extend their ranges to higher latitudes and altitudes; although, for islands, immigration from other landmasses will be interrupted to some extent by the sea barrier. Species which currently have wide latitudinal ranges, already encounter considerable temperature variation and are, in a sense, preadapted to cope with temperature change. Those with restricted climatic ranges, particularly montane and cold-adapted species, are likely to be more vulnerable (Butterfield & Coulson 1997).

Predicting insect response to elevated temperatures is largely based on field and laboratory studies carried out over a range of temperatures, either on single species (e.g. Andrewartha & Birch 1954; Danilevskii 1965; Hill & Hodkinson 1996) or on species combinations (e.g. Park 1948; Birch 1953; Davis *et al*. 1998; Masters *et al*. 1998). In addition, fossil evidence indicates that insect distributions have responded in the past to climate change (Coope 1970, 1987, 1995; Ashworth 1997). There is, for example, increased attack frequency and a greater
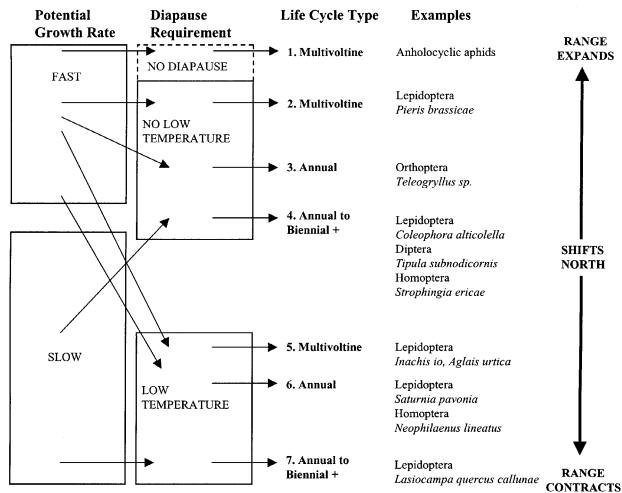
Fig. 2 Simplified model of insect response to environmental warming. The growth period is assumed to be during the summer and the single diapause during the winter. The low temperature requirement for diapause indicates where temperatures lower than those favourable for morphogenesis are needed for successful life-cycle completion. Through combining fast/slow growth rates with temperature-related diapause, predictions as to the life cycle of a species and its response to climate change through changes in its distribution (range) are possible. Fast growing, non-diapausing species are likely to be multivoltine and will respond the greatest to temperature elevation through expanding their ranges. Fast growing species which are not dependent on low temperatures to induce diapause are likely to be multivoltine or annual and will respond through range expansion. However, those fast growing species which do need low temperatures for diapause (again multivoltine or annual) are likely to respond to climate change with some range contraction. Slow growing species which need low temperatures to induce diapause are likely to be unable to expand their ranges and may be detrimentally affected by climate change. This simple framework could be applied to a large range of insects, and through knowing two parameters (growth rate and diapause requirement) potential range/distribution changes estimated.

diversity of insect damage per host plant species recorded on fossil leaves in south-western Wyoming during the late Palaeocene-early Eocene global warming interval (Wilf & Labandeira 1999). Together, these observations provide evidence that both the diversity of insect herbivores and the intensity of herbivory increases with rising temperatures at constant latitude.

Predicting future insect population dynamics and distributions is complex even at the level of the individual, let alone that of interacting communities. As already noted, life-cycle timing in different insects depends on a wide variety of responses to both abiotic and biotic factors and, in most cases, the life cycle encompasses two very different physiological stages (growth and diapause); higher temperatures may result in increased

growth rates but it is likely to prolong the diapause stage (Tauber *et al.* 1986). It is obviously not possible to investigate every insect life cycle nor, even, every potential pest species to determine this variation, but predicting future distributions based on single species studies may be unrealistic as spatial patterns are, at least partly, determined by interactions with other species (Davis *et al.* 1998). Some broad categories of response of different insect life-histories can be suggested (Fig. 2). Based on physiological adaptations, these categories overlay and add complexity to the earlier discussion of insect life cycles in relation to plant growth strategies.

Our optimism that the approach suggested in Fig. 2 has validity is partly based on the fossil record which suggests that many beetle species, and possibly insect species in general (Coope 1995), have retained similar climate requirements over thousands of years. Many of the species that were cohabiting 100 000 years ago are still living together today, under similar climatic conditions (Coope 1978). There are, however, also many present-day examples of insect species exhibiting latitudinal clines in developmental response, indicating physiological adaptation (Danilevskii 1965; Masaki 1978), as discussed further below.

Growth stage: effects of higher summer temperatures

Most temperate insect herbivores have their main growth period during the warmer part of the year. The temperature range favourable for growth differs between species and is often related to climatic range and habitat. Within this favoured temperature range, temperature elevation increases the speed of development during the growth phase but the rate of increase differs between species. This again relates to ambient temperatures encountered in the field (Andrewartha & Birch 1954; Danilevskii 1965; Butterfield & Coulson 1997).

Future climatic warming will affect temperate annual and multivoltine species in different ways and to differing degrees. In the case of multivoltine species, such as the Aphididae (life cycle Type 1, Fig. 2) and some Lepidoptera, e.g. *Pieris brassicae* (Type 2, Fig. 2), higher temperatures should, all other things being equal, allow faster development times, probably allowing for additional generations within a year (Pollard & Yates 1993). Many of these species will expand their geographical ranges to higher latitudes and altitudes, as has already been observed in a number of common butterfly species (Pollard *et al.* 1995; Hill *et al.* 1999; Parmesan *et al.* 1999). However, the effect of higher temperature on the overall abundance of herbivorous insects remains unknown in the absence of equivalent data on the responses of their natural enemies (e.g. see Davis *et al.* 1998).

The responses of annual insect species to warming may be predicted from their feeding and life-cycle strategies (an example is shown in Fig. 3). Species with annual life cycles generally develop faster than those with longer life cycles. This rate of development will enable a more rapid response to a change in, for example, temperature. In species where the growth rate/temperature response curve is steep, as in *Saturnia pavonia* in Fig. 3, higher temperatures during growth will have the favourable effect of reducing time spent in larval and nymphal feeding stages which are the periods typically exposed to predation (Bernays 1997). Such species should also be able to extend their distributions to higher latitudes and altitudes. In species with a prolonged larval period (e.g. *Lasiocampa quercus callunae*, Fig. 3), where the growth rate/temperature response is shallow and the favourable development temperature range both low and restricted (e.g. *Tipula subnodicornis*, Butterfield 1976a) (life cycle Type 4, Fig. 2), the southern edge of the present geographical range may become too warm resulting in a northwardly movement of the species' distribution. This is also likely to be the case for species with biennial, or longer, cycles, where there is prolonged exposure (through slow development time preventing rapid adaptation) to climate change. In such cases, migration to higher latitudes might be the only option for the species.

The slow growth of insect herbivores at high latitudes has been suggested to be a strategy linked to the low digestibility of cellulose at temperatures below 13 °C (Remmert 1980). Although few insect herbivores produce cellulases (Terra 1990), Remmert's observation is probably relevant to some Tipulidae, a group well represented in montane and Arctic regions (Coulson & Whittaker 1978; Coulson & Butterfield 1985; Coulson 1988), where a number of species have cellulases or harbour symbiotic cellulose-digesting bacteria (Griffiths & Cheshire 1987; Abe & Higashi 1991). At all latitudes, insect herbivores that chew vegetation but with relatively little damage to the cell walls have to ingest large proportions of cellulose (Abe & Higashi 1991; Martin 1991; Hochuli 1996). The bulk of plant material that has to pass through the insect gut to provide adequate nitrogen must impose restrictions on the growth rate and the extent to which these insects can respond to elevated temperature. Where species such as *T. subnodicornis* or *L. quercus callunae* have adopted the slow-growth strategy, it seems unlikely that the adaptation could be easily reversed under warmer climatic conditions. These species will probably suffer contraction of their present geographical ranges if summers become warmer, as the scope for their movement to higher latitudes or altitudes is, in many cases, limited.
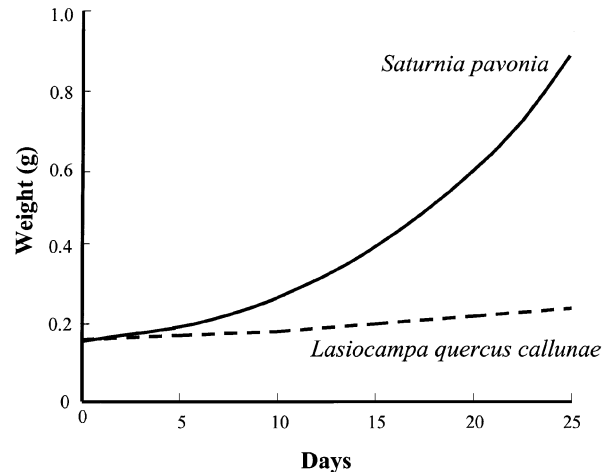
Fig. 3 Growth rate curves for *Saturnia pavonia* and *Lasiocampa quercus callunae* feeding on *Calluna* sp. at 20 °C in mid summer (July). The species with an annual life cycle, *S. pavonia*, exhibits an exponential increase in size over a period of 25 days in comparison with the almost negligible increase in size displayed by *L. quercus callunae*, a species with a longer biennial life cycle. *Saturnia pavonia* will develop quicker and will be probably more responsive to climate warming through changing its distribution. *Lasiocampa quercus callunae* has a shallow growth curve and will take longer to develop and so will be restricted in its response to climate change.

Diapause stage: effects of higher winter temperatures

Non-diapausing, frost-sensitive species and those which are able to overwinter in their active stages, such as the aphid *Myzus persicae* (Bale *et al.* 1988) (life cycle Type l, Fig. 2), show increased winter survival in warm winters. These species can be expected to increase population densities and expand their geographical ranges to higher altitudes and latitudes as average temperatures increase. Most temperate insect species diapause during winter, some in the inactive egg or pupal stages, others as larvae, nymphs or adults in reproductive diapause. When diapause occurs in the inactive stages, it often involves a profound drop in metabolic rate linked to an increase in cold hardiness (the ability of an organism to survive at low temperatures; Leather *et al.* 1993). In larval diapause, probably more prevalent in below-ground herbivores protected from low temperatures, feeding may continue and forward development slow down rather than cease. In univoltine species, diapause is an obligatory part of the annual life cycle, whereas in multivoltine species it is facultative and occurs in response to an environmental trigger such as decreasing day length or increasing night length (Tauber *et al.* 1986). Temperatures favouring completion of a winter diapause are often lower than the favourable range for growth (Fig. 4, Danilevskii
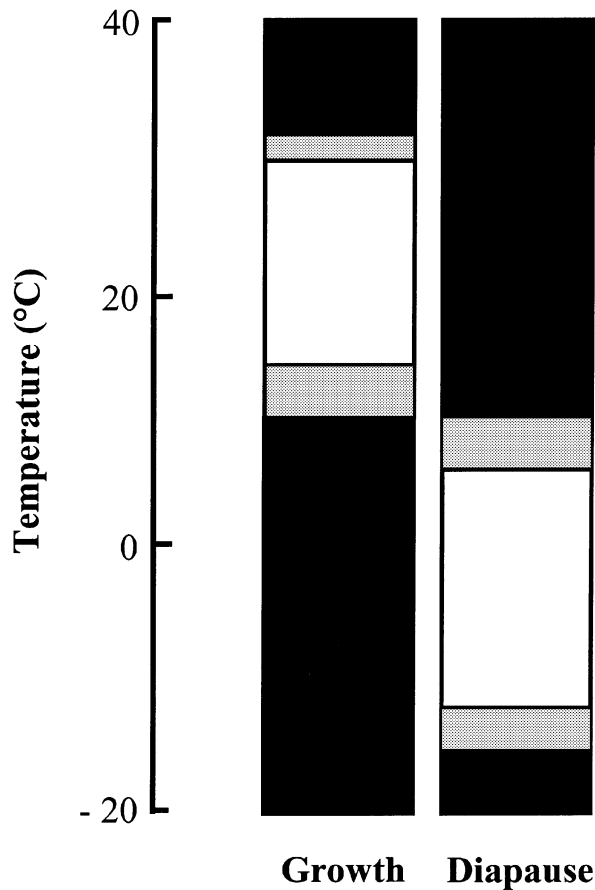
Fig. 4 Temperature requirements for growth and diapause in *Saturnia pavonia*. Favourable temperature ranges are shown by the white bars, lethal temperature ranges are shown by the black bars, and depressing temperature ranges are shown by the grey bars (adapted from Danilevskii 1965). There is a restricted 'window' for growth (white bar), with an upper and lower threshold beyond which development does not occur. To prevent imminent death when temperatures drop below *c.* 5 °C, *S. pavonia* enters diapause; however, death follows if the temperature continues to drop.

1965), reflecting summer and winter temperatures within the geographical range.

The geographical ranges of some species can be limited by the degree of frost resistance of their winter stages and, in this case, their northern limits coincide with the isotherms of their winter minima (Uvarov 1931; Danilevskii 1965). It is probable that the geographical ranges of these species will expand northwards in a warmer climate. In other species, warmer winters will exceed the threshold for diapause at the southern edge of the range and distributions will shift north. For instance, winter diapausing adults of the butterflies *Inachis io* and *Aglais urticae* (Type 5, Fig. 2) both show decreased survival rates at 10 °C compared with 2 °C and this is

more marked in *I. io* than *A. urticae* (Pullin & Bale 1989). The southern edge of the geographical range of *I. io* approximates to the 10 °C January isotherm and that of *A. urticae* does not far exceed it (Bryant *et al.* 1997). The southern edges of the geographical ranges of both these butterflies will retract northwards if the winters become warmer. The distribution of *I. io*, which is less tolerant of long periods of low temperature than *A. urticae* (Pullin & Bale 1989), will continue to expand northwards and its geographical range as a whole will shift. *Aglais urticae*, which already exists as far north as the North Cape, Norway (71°10′ N, 24°11′ E), can expand no further (Bryant *et al.* 1997), so although the species may become more abundant in the north, its range will in fact decrease.

For simplification, species which diapause in summer (aestivation) have been omitted from Fig. 2, but it should be noted that these species are not confined to arid areas and that they contribute to the insect fauna as far north as 60° N (Masaki 1980). Species that have a synchronized adult emergence in autumn are unlikely to be affected by increased summer temperatures as diapause is usually prolonged by high temperature (Masaki 1980; Buse & Good 1996) and release, as in *Tipula pagana* (Butterfield 1976b), may be under photoperiodic control (Tauber *et al.* 1986). However, typical of many summer diapausing species (Masaki 1980), *T. pagana* also has a winter egg diapause (Butterfield & Coulson 1988), where winter temperatures may be important for diapause promotion (Fig. 2).

Diapause: recent progress from field and laboratory research

Studies on annual or biennial insect herbivore species, such as the spittlebug *Neophilaenus lineatus*, the moth *Coleophora alticolella* and the psyllid *Strophingia ericae*, have shown that diapause not only plays an important role in promoting seasonal synchrony, but also buffers the effects of temperature differences, allowing some insect species to exist over wide geographical ranges. In *N. lineatus*, for instance, the eggs overwinter in diapause that ends in late winter. Research on *N. lineatus* over altitudinal transects found that eggs hatch later at higher altitude (Fielding *et al.* 1999), thus nymphs at high altitude appear later in the season. Nymphal development was found to occur in relation to spring temperatures, where nymphs experienced a similar thermal regime across a wide altitudinal range, thus similar development rates irrespective of altitude. The later emergence of adults at high altitude is then the result of late egg hatching and not slowed nymphal development (Whittaker & Tribe 1996; Fielding *et al.* 1999). This

familiar life-history pattern is also exhibited by *Philaenus spumarius*, where egg hatching in winter in experimental warmed plots (3 °C above ambient temperatures from November to the following April) was found to be earlier than that in unwarmed plots (Masters *et al.* 1998). There is a similar response to accumulated spring temperature sum in *O. brumata* eggs, causing earlier hatching in warmer springs. However, the autumn pupal diapause in this species is prolonged at higher temperatures, so the life cycle as a whole is not shortened by increase in temperature. Synchronization between oak budburst and egg hatch in *O. brumata* will not be affected by a warmer climate (Buse & Good 1996), a conclusion contrary to the often predicted phenological asynchrony between host plant and insect herbivore, as discussed previously.

At 556 m a.s.l., *S. ericae* responded to the direct effects of elevated temperatures in cloches with increased population densities and earlier hatch and, in the second year of the experiment, earlier adult emergence periods (Miles *et al.* 1997). The earlier timing of adult emergence was somewhat surprising because, in general, this species shows close synchrony of emergence date over altitudinal transects (Fielding *et al.* 1999). It does, however, agree with the experimental evidence that the short photoperiod effect, which restricts development of the biennial fifth instars in autumn, has disappeared by January (Miles *et al.* 1998). A specialized adaptation in the life cycle is the prolonged hatching period of the first instar, especially in the biennial cycle when first instar nymphs are present throughout the year (Hodkinson 1973). This is a likely consequence of some eggs hatching in summer and autumn of the year they are laid while others enter diapause and overwinter as eggs.

Coleophora alticolella overwinters in larval diapause and, in common with *S. ericae*, short photoperiod acts to maintain diapause in the early stages. There appears to be a polymorphic response to day length in diapause termination. After winter chilling, there was no difference between the mean emergence dates of larvae subjected to 15 °C on L : D 18 : 6 or 15 °C on L : D 6 : 18 from 1 February but the number emerging on the longer photoperiod (18 : 6) was three times higher than on the shorter (6 : 18). With 6 h day length, greater than 50% of the population remained in larval diapause (Butterfield *et al.* 1999). Some of the population always remained in diapause in a wide range of experimental chilling and photoperiod regimes and it is possible that this species could extend its life cycle to a second year, as in other seed-eating species where seed set may be irregular (Bakke 1971). In the case of *C. alticolella*, an adaptation of this kind could be important in allowing survival of populations in the middle of the altitude range where seeds of the host plant *Juncus squarrosus* are

sometimes totally consumed by larvae of *C. alticolella*, leading to heavy larval mortality (Randall 1982, 1986).

Most temperate insects will be little affected by warming and only the specialist cold-adapted species will be adversely affected. Where field temperatures have been manipulated or studies made along a transect, hatching or emergence has been earlier at higher temperatures (Buse & Good 1996; Miles *et al.* 1997; Masters *et al.* 1998), but the diapause response has tended to counteract the effects of an earlier start to the life cycle. Where release from diapause is under photoperiodic control, as in the winter diapause of *Cacopsylla moscovita* (Hill & Hodkinson 1996) or the summer diapause of *Tipula pagana* (Butterfield 1976b), temperature rise will have least effect. Despite this, there will still be many species that respond unpredictably to higher temperatures (Lawton 1995). This is true even for species that might be assumed to be stenothermal and cold-adapted; e.g. *Tipula montana*, an Arctic and montane biennial species that is not usually found below 600 m a.s.l. in Britain, has recently been found as low as 350 m a.s.l., where most of the population has an annual life cycle (Todd 1996). The effects of temperature (particularly in the case of altitudinal gradients) cannot be considered in isolation from other factors that also change with altitude. For example, the rates of parasitism by *Phobocampe neglecta* (Hymenoptera: Ichneumonidae) in *O. brumata* on heather moorlands averaged 27% at sea level but declined to zero at higher altitudes (Kerslake *et al.* 1996). This was probably due to increasing wind speeds reducing parasitoid foraging efficiencies (Messing *et al.* 1997). Furthermore, laboratory manipulation experiments have shown that, even with simple three-species assemblages, the presence of other species can shift the occupied temperature range from the single species preferendum (Davis *et al.* 1998). Although some species, especially those in ancient groupings that have already encountered major climatic changes, will respond to climate change predictably (Coope 1987), there are many species that will not. In these cases, population dynamics across the new geographical ranges will be unpredictable. Insect herbivores will undoubtedly contribute to more pest outbreaks, especially in cases where they have expanded their ranges more rapidly than their enemies, as shown in the Palaeocene-Eocene warming period where the diversity and intensity of insect herbivory increased (Wilf & Labandeira 1999).

Despite these complexities, a range of insect herbivore species was classified within the framework of Fig. 2. This figure is in itself too highly simplified to reflect the probable variety of response to a warmer climate within the Insecta as a whole (e.g. *O. brumata* has two diapause stages), but we suggest that this approach, using a broad classification, provides a useful basis for predictive

modelling of insect response to climate change. Through measuring, or taking from any existing literature, the relative growth rates and the diapause requirements of an assemblage of insect herbivores, the framework presented in Fig. 2 can be applied to predict range expansion or contraction, an important consideration for potentially invasive species.

Distribution: evidence from past responses to climate change

The effects of temperature on insect development rates and voltinism will be reflected in changes in geographical distributions. This likelihood is supported by fossil evidence; many insects have tracked climate change rather than adapted to it (Coope 1978). By allowing for different rates of migration in plants and insects, it should be possible to predict future changes in the distributions of insects alongside climatic predictions. Despite the fossil evidence for absence of adaptation, many studies have shown that some insects, at least, have evolved geographical strains with physiological adaptations appropriate to the latitude at which they are living (Danilevskii 1965; Masaki 1967; Tauber *et al*. 1986). Indeed, there are examples where strains have diverged to the extent that they are genetically incompatible, indicating incipient speciation (e.g. *Drosophila melanogaster* populations, Korol *et al*. 2000). Selection experiments have shown that major changes in both the percentage of individuals in a population that enter diapause and in the day length shortening required to trigger diapause can occur within 3–15 generations (Masaki 1978; Delinger 1986; Pullin 1986).

The fossil record is biased towards Coleoptera; their heavily chitinized exoskeletons resist decay (Coope 1978). Coleoptera is probably not the best taxon predictor for the Insecta as a whole as it largely evolved and diversified before the Quaternary. However, psyllid species feeding on willow (*Salix*) have been shown to replace each other along altitudinal gradients (Hill & Hodkinson 1995; Hill *et al*. 1998) in a similar way to carabid species (Butterfield 1996) and, in this instance, predictions of future herbivore distributions would also be closely linked to different temperature change scenarios. Species living in closely packed communities, and where niche space is defined by thermal regime, will respond more predictably to climate change while those in which the niche is limited by other abiotic or biotic factors will be less predictable. Predicting a change in a species's distribution is relatively easier than predicting its population dynamics across its range. At any locality, the population density of the insect herbivore will depend not only on its own capacity for increase, but also on the presence and abundance of its predators and parasites (Randall 1982).

Distribution: migration and movement

Temperature thresholds for insect flight vary both among and within species, with season and also with region (Robert & Rouzé-Jouan 1976; Wiktelius 1981). Different thresholds have also been described for different phases of flight activity. For example, in the aphid *Aphis fabae*, 17 °C is required for take-off (Johnson & Taylor 1957), 15 °C for sustained upward flight, 13 °C for horizontal flight and 6.5 °C for wing beating (Cockbain 1961). Climate warming would advance the time of year at which the flight thresholds for all insects are first reached and increase the possibility of early immigration (e.g. aphids: Woiwod & Harrington 1994; Fleming & Tatchell 1995; Zhou *et al*. 1995; moths: Woiwod 1997). In summer, upper thresholds might be reached more frequently, limiting flight opportunities. The concept of an optimum temperature above which flight activity is gradually reduced is not predicted by Taylor (1963) who found little change in flight activity between the upper and lower thresholds of a wasp, an aphid, a beetle and two moth species. There are other meteorological factors that influence insect flight, especially wind speed and direction, rainfall, humidity and insolation, but too little is currently known as to how these may change in the future, and what their impact will be on insect flight, to warrant discussion.

Inevitably, there are optimal and threshold temperatures for insect walking, an important factor in very local redistribution and for the spread of pathogens. Below the optima, climate warming will enhance movement, above it will be detrimental. Regional and seasonal variation in thresholds is likely (e.g. Bodenheimer & Klein 1930 cited in Uvarov 1931; Aitchison 1978) thus making prediction of walking responses to climate change difficult. Low temperature can prevent essential movement to new feeding sites and lead to mortality due to starvation (e.g. aphids: Harrington & Taylor 1990). This is one of many reasons that milder winters lead to greater survival. Considering aphids, one consequence of enhanced movement is increased secondary spread of viruses to crops (Harrington *et al*. 1994).

Populations of herbivorous insect species that exhibit wing polymorphisms that are, at least partially, controlled by environmental factors (e.g. aphids, planthoppers and crickets) tend more towards the alate (winged), as opposed to apterous (wingless) or macropterous (large winged) forms as opposed to brachypterous (small winged) condition as density increases. Many insects that do not have such overt dimorphism have winged adults that differ in their propensity for flight as a result

of flight muscle polymorphism, with stronger fliers often appearing in response to crowding. Aphids, an insect taxon most likely to be affected strongly by temperature change (Kiritani 1997) as a result of their low developmental threshold, low developmental constant and multivoltinism, have pronounced environmentally controlled polymorphism. In general, warmer conditions lead to rapid population build up resulting in rapid alatae production. However, this may be modified by reduced wing production, a physiological effect of higher temperatures (and of low temperatures: Parish & Bale 1990), thus reducing the aphids ability to disperse in response to crowding. This could, however, be advantageous during winter; even with global warming the threshold temperatures for flight are rarely exceeded and apterous aphids are more fecund than alatae. Anholocyclic aphids, unlike the overwintering eggs of holocyclic species, do not have a winter diapausing stage and are not required to pass through one or more wingless generations on the winter host prior to host alternation. The former can therefore colonize crops more quickly when spring conditions become favourable, and earlier flights are known to occur after milder winters (Harrington *et al*. 1995). Such relationships are most likely to result from improved survival leading to larger populations and hence earlier production of alatae as a result of crowding.

Discussion

The direct effects of temperature on insects are likely to differ among species, depending on their existing environments and life-histories, and their ability to adapt. Flexible species that are polyphagous (e.g. *O. brumata*), occupy different habitat types across a range of latitudes and altitudes, and show high phenotypic and genotypic plasticity. Such species are less likely to be adversely affected by climate change than those species, such as psyllids in Arctic regions, occupying narrow niches with highly constrained life styles in extreme environments. Very little is currently known of insect capabilities for genotypic change in response to climatic selection pressures, although molecular techniques may soon allow rapid progress. Similarly, adaptation to climate change by dispersal has been neglected and relatively little is known about the dispersal abilities of many insect herbivores (but see Speight *et al*. 1999). The ability of insect herbivores to adapt to climate change, through phenotypic flexibility and rapid evolutionary responses to strong selection, could mitigate the adverse effects of changing climate in many species.

Direct effects of temperature increases on insects are likely to differ among habitats. Effects are likely to be most pronounced in the Arctic and other extreme environments and least in the tropics, although the interaction between temperature and other factors such as rainfall may become important in tropical regions. It is important to highlight unpredictability: the increase in likelihood of extreme events (e.g. storms, late frosts and droughts) may outweigh small overall increases in mean temperature. Increases in variability may have larger effects than small increases in means. A distinction must be made between the effects of a rise in mean temperature and the effects of an increase in the likelihood or nature of extreme events. In many species, it is not small increases or decreases which affect performance and survivorship, it is the likelihood of experiencing sudden frosts after periods of warm weather. Thus, it is not the magnitude of change that is important, but the unpredictability in the system. Additionally, direct effects are difficult to disentangle from indirect ones, particularly in the interpretation of phenological responses and for effects along altitudinal vs. latitudinal gradients: parameters other than temperature change with altitude and factors such as wind speed may be critical.

The effects of temperature on insect performance may also vary on different host plants. Phenological windows differ, even for the same species feeding on different hosts. Climate may have less influence on species feeding on determinate compared to indeterminate plant species. The ability of insects to deal with a range of different host plants, including low quality ones, may indicate their ability to cope with climate change. Insect species that show a degree of compensatory feeding may adjust to climate change-induced phenological distribution.

Temperature rise is likely to affect insect morph determination and movement through a number of mechanisms. The complexity of the interactions among the abiotic and biotic components of climate change at the species level may preclude determination of the outcome of such changes at the community level. For example, a simulation of the effects of climate change on the population dynamics of an aphid found that with increased temperature the species became more abundant but, in some circumstances, displayed greater variability indicating that the population was less stable (Zhou *et al*. 1997). Nonetheless, empirical analyses of long-term data indicate that changes in flight phenology, compatible with expectations of the effects of climate change on movement, are already apparent.

Unknowns, conclusions and priorities for future research

To understand the direct effects of climate change on insect herbivores we need to realize: (i) insects already encounter and cope with large natural spatial and temporal variations; (ii) insect responses to climate

change may be specific to site (e.g. altitude), species (e.g. polyphagous vs. monophagous) and host plant (e.g. high quality vs. low quality); and (iii) factors such as temperature may have conflicting effects. Individuals may develop faster at higher temperature and survival may even be enhanced, but these insects may consequently have lower adult weight and fecundity. We must assess the overall impact of different factors and not presume that the measurement of a single performance parameter tells us all we wish to know. It is almost impossible to 'know all the answers', but three significant unknowns have been illustrated by this review:

1 During a number of studies on development rates of species along altitudinal transects, development has been found to be temperature-independent in field studies, but temperature-dependent in the laboratory (Butterfield 1976a; Coulson *et al.* 1976; Fielding *et al.* 1999). It is well documented that Lepidoptera caterpillars manipulate their thermal environment behaviourally (May 1976; Heinrich 1977; Porter 1982; Bryant *et al.* 2000) and the bug *N. lineatus* may regulate its thermal regime via its surrounding spittle (Whittaker 1970). The apparently synchronous development of the soil-inhabiting tipulid *Molophilus ater* over 400 m altitude on Great Dun Fell, Cumbria, UK (54°41′ N, 2°27′ W) (Coulson *et al.* 1976), is more difficult to explain.

2 In many annual insect life cycles, diapause maintenance and the timing of its release will mitigate the effects of higher temperatures on the growth period. The interaction of temperature and day length during the diapausing stages is not well understood for many common species and, especially in the case of pests or potential pest species, requires further research effort. Insect life cycles in which more than one diapause period occurs have been little studied. Masaki (1980) has suggested that many summer diapausing species also have a winter diapause stage but there are few cases where both diapause stages have been studied in conjunction.

3 In many species, niche width is probably determined, at least in part, by temperature regime. Although we often know which species replace each other along climatic gradients, there is much less information on why one species replaces another.

Accepting that there are still many challenges facing biologists in predicting and monitoring the impacts of climate change, including addressing the unknowns above, we suggest that future research must take into account the following:

1 Predicting the direct effects of climate change on insect herbivores needs to take account of phenotypic and genotypic flexibility.

2 Global change parameters operate in concert against a background of local environmental variation. The evaluation of any changes in insect herbivore populations should be studied within these contexts. Interaction between the different climate change factors needs considerably more detailed investigation. The direct effect of temperature may be modified by increased precipitation; this, in turn, is likely to affect relative humidity, which is important for physiological functions, e.g. reproduction (Cammell & Knight 1992). Additionally, direct effects of climate change on insect performance need to be set in a wider context and attention given to how direct effects of temperature interact with other factors, particularly natural enemies (probably important but little studied) and host plant condition.

3 Little is known about long-term population-level responses of herbivores to global environmental change.

4 Research effort needs to be expanded to other biological systems (e.g. marine and freshwater) and different herbivore groups. Most work has been conducted with terrestrial insects.

5 Research can be conducted on only a small fraction of the Earth's biota. It must therefore focus on keystone species, those of particular importance to the structure and functioning of natural and managed ecosystems.

Acknowledgements

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