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NEW PERSPECTIVES

Climate change and phenological asynchrony

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It is important for herbivorous insects to synchronise their development with that of their host plants. For many insects, a critical stage in the development of plants is bud-burst (Dixon, 1976; Watt & McFarlane, 1991; Komatsu & Akimoto, 1995). Much of the debate about the effect that climate change may have on insect abundance is concerned with its possible differential effect on bud-burst in plants and egg hatch in insect herbivores (Dewar & Watt, 1992; Harrington *et al*., 1999; Watt & Woiwod, 1999). In their recent review, Watt and McFarlane (2002) challenged the conclusion of Buse and Good (1996) that climate change has no effect on phenological synchrony. Buse and Good used saplings growing in pots and Watt and McFarlane argued that the roots of these saplings are likely to have experienced similar temperatures to the rest of the plant, which is unlikely to be the case for deep-rooted mature trees. Although an interesting point, it is worth asking whether synchrony *per se* is the issue to be addressed. What is possibly more important is the mechanism(s) by which herbivores and hosts track the seasons and whether herbivores can adapt quickly to changes in the phenology of their host. The fact that insects are well synchronised with their host plants indicates that adaptation is possible. Compared with many other insects, aphids are a good model group for exploring this problem as the mechanisms by which they track the phenology of their host plants and their population dynamics are well understood.

There is a lot of variability in both the time of egg hatch and bud-burst, both within and between years. Eggs that hatch at the time of bud-burst tend to be fitter than those that hatch earlier or later (Dixon, 1976). In addition, the time of egg hatch appears to be inherited (Komazaki, 1986; Mittler & Wipperfurth, 1988; Komatsu & Akimoto, 1995). Both times of bud-burst of sycamore saplings and egg hatch of the sycamore aphid are influenced by spring temperatures (Chambers, 1979). For both trees and eggs, there is an inverse relationship between the number of chill days experienced and the thermal time from some date in spring to bud-burst and egg hatch (Mittler & Wipperfurth, 1988; Murray *et al*., 1989). That is, both buds and eggs tend to remain dormant until they experience their chilling requirement, then the time to bud-burst or egg hatch is a function of the intensity of the chilling they have experienced and subsequent spring temperatures. Although the lower developmental thresholds of bud development in sycamore saplings (0 °C) and sycamore aphids (5 °C) in spring differ (Chambers, 1979), egg hatch and bud-burst are nevertheless synchronised (Dixon, 1976). That is, although the tracking mechanisms used by the plant and insect differ in detail, synchronisation is possible. Selection would appear to have resolved a complex optimisation problem.

In their review of this subject, Harrington *et al*. (1999) highlighted what they regard as research priorities. One such priority is to determine how changes in synchronisation affect population dynamics. This is important because it has implications for the evolution of many herbivore–plant interactions. In the case of the sycamore aphid, there is an inverse relationship between abundance in spring and autumn – the *see-saw* effect. Low numbers in spring are followed by high numbers in autumn and vice versa (Dixon, 1970; Dixon & Kindlmann, 1998). If climate change affects bud-burst and egg hatch in this system differentially, it is likely that the mortality of the aphids hatching in spring will be higher and the average fitness of the survivors lower (Dixon, 1976). Climate change-induced asynchrony in the frequency distributions in time of bud-burst and egg hatch in any one year is likely to be slight and any negative effect on aphid numbers will be compensated for within the year due to the dynamics of the system. In addition, proportionally more of the survivors will be individuals with inherited responses that enable them to track more closely the phenology of their host plant. These aphids are likely to mate with one another and as a consequence the following year proportionally more of the eggs hatch in synchrony with bud-burst. That is, selection will correct for any asynchrony between egg hatch and bud-burst.

Predictions of models that attempt to determine the effect of climate change on the abundance of an insect, which do not include the mechanisms by which the insect's abundance is regulated and how selection is likely to shape its life-history strategy, are unlikely to be realistic. For tree-dwelling aphids, in which the processes acting at both the

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individual and population levels are fairly well understood, the evidence tends to indicate that the adverse effect of climate change is unlikely to be as threatening as is so often suggested.

Hatchlings of herbivorous insects generally are likely to suffer a very high mortality if egg hatch is not associated closely with some critical stage in the development of their host plants. In the case of the winter moth on oak, winter disappearance on average accounts for 86% of the total mortality and is attributed mainly to asynchrony between egg hatch and bud-burst (Varley *et al.*, 1973). This being so, a genotype whose egg hatch is only slightly better synchronised than the average will be at a selective advantage; however the wide host range of the winter moth possibly constrains a closer association with oak phenology in this case. That is, in host-specific herbivorous insects, in which mortality at some critical stage in their development accounts for most of the total mortality, a slight decrease in this mortality results in a very large increase in fitness. Thus, for insects in which synchronisation between budburst and egg hatch is important, there is likely to be a very strong selection pressure maintaining close synchronisation.

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