Abstract  Plants can have a significant impact on the fitness and efficacy of natural enemies. These interactions are widespread and suggest that the influences on the population dynamics of insect herbivores cannot be simply divided into “bottom up” and “top down”. Several questions remain little studied in this field. Firstly, to what extent can plants affect the interactions between insects and their pathogens? Secondly, what are the effects of variation within natural enemy species on host/enemy/plant interactions? Finally, if plant/pathogen interactions can occur, do pathogens have increased fitness on the locally abundant food plant of their host? This study explored the influence of three host plant species of the polyphagous winter moth, *Operophtera brumata*, on infections caused by two geographic isolates of the winter moth nucleopolyhedrovirus (NPV) collected from distinct winter moth habitats. Insects were infected on excised leaf tissue of common oak, *Quercus robur*, Sitka spruce, *Picea sitchensis*, and heather, *Calluna vulgaris*. Parameters fundamental to the basic reproductive rate of the pathogen were estimated: these being infectivity, speed of kill and the yield of virus per insect. Leaf nitrogen and phenolic content were measured as indicators of host plant quality for the three plant species: oak had the highest levels of nitrogen and also the highest levels of phenolic compounds. Heather had higher levels of phenolic compounds than Sitka spruce. Host plant did not affect the infectivity of either isolate but insects that ingested virus on oak foliage died sooner and yielded more virus than insects that ingested virus on Sitka spruce or heather. The effect of host plant species on pathogen yield varied between the two isolates of the NPV but not as predicted by our adaptive hypothesis. The interactions between virus and food plant are discussed in relation to host and pathogen population dynamics.

Keywords  Baculovirus · Insect pathology · Population dynamics · Tritrophic interactions

Introduction

Plants can have substantial effects on the survival of herbivores by altering their susceptibility to natural enemies (Price et al. 1980; Denno and McClure 1983; Hare 1992; Williams 1999). Host plants may directly affect the mortality or abundance of enemies through morphological features such as trichomes or domatia (Farrar and Kennedy 1991; Walter and O’Dowd 1992). In addition, plants can indirectly affect natural enemies via their effects on herbivore behaviour or physiology. For example, plant secondary metabolites ingested by herbivores can have significant effects on parasitoid survival and fecundity (Campbell and Duffey 1979; Thorpe and Barbosa 1986). The fitness of natural enemies can also be correlated with the growth rate of herbivorous prey: smaller, less well-nourished prey can affect the growth and development time of predators (Orr and Boethel 1985). Alternatively, faster growing prey may be either less vulnerable to parasitoid attack or better able to encapsulate pathogens or parasitoids (Benrey and Denno 1997).

However, few studies have empirically demonstrated the importance of the interactions between natural enemies and host plants for herbivore populations in the field (but see Van Nouhuys and Hanski 1999). The impact of damage-induced changes in foliar chemistry on
insect viral pathogens has been examined, and changes in plant chemistry can affect herbivore population dynamics but only if these changes overlap with larval feeding period (Foster et al. 1992; D’Amico et al. 1998). In general, there have been few empirical studies of the interactions between food plant and pathogens, and most have concentrated on the effects of plant chemistry on infectivity (reviewed in Duffey et al. 1995), which is but one of several potential factors determining the population dynamics of host and pathogen.

Few tritrophic studies outside the biological control literature (e.g. Kruse and Raffa 1997) have considered the effects of natural enemies’ genotypic variation on their efficacy or on interactions between enemy, host and plant. Without an understanding of this variation it is not possible to determine whether specific tritrophic interactions are pre-determined by the ecology of host and habitat or whether they are changeable and are a consequence of evolutionary interactions. Insect hosts vary in their susceptibility to attack by pathogens or parasitoids (e.g. Briese and Mende 1981) and resistance can evolve in response to selection (Kraujięveld and Godfray 1997). Variation in resistance of hosts can either be genetically associated with different populations on different plant species (Hufbauer 2001) or a physiological consequence of the chemistry of the food plant (Duffey et al. 1995). The evolutionary responses of natural enemies to this variation in resistance are less well known but, in either case, plant associated effects may produce enemies that are locally adapted to the dominant environmental conditions.

The winter moth, *Operophtera brumata* L., is a polyphagous herbivore that often shows out-breaking population dynamics. The taxonomic range of its host plants is very wide: in lowland Britain it is commonly found on oak, *Quercus robur* L. and also a wide variety of broad-leaved species including orchard trees (Varley et al. 1973; Holliday 1977). In Scotland winter moth has made a recent host shift on to Sitka spruce, *Picea sitchensis* (Bong.), and regularly occurs on heather moors feeding on heather, *Calluna vulgaris* (L.), and bilberry, *Vaccinium myrtillus* L. The dynamics of winter moth on oak (at Wytham Woods near Oxford) were the subject of a classic life-table study and are well understood (Varley et al. 1973). In contrast to the more bounded oak populations, winter moth populations regularly outbreak in young Sitka spruce plantations (Stoakley 1985; Hunter et al. 1991) and on heather moorlands (Kerslake et al. 1996). Outbreak densities of 500–1,400 m⁻² have been recorded on some moorland sites and can result in long-term changes in the plant community (Kerslake et al. 1996). The causes of these outbreaks and the factors which ultimately limit them, are as yet unknown (Hunter et al. 1991; Kerslake et al. 1996; Kerslake and Hartley 1997), although baculovirus epidemics have been observed to follow several outbreaks (Embree 1966; Stoakley 1985; J. Cory and R. Hails, personal observation; B. Raymond, personal observation). Given the variation in the host plants consumed between and within winter moth populations, there is a great deal of potential for tritrophic interactions to influence the dynamics of both insect and pathogen in the field.

Baculovirus epidemics are frequently reported following outbreaks of Lepidoptera (Entwistle and Evans 1985; Tanada and Fuxa 1987). High host density and the resulting enhanced transmission rates could be responsible for the re-emergence of typically rare and insignificant pathogens (Myers 1988). Alternatively, baculoviruses are plausible agents for driving the fluctuation in density of many Lepidopteran species (Anderson and May 1981; Dwyer et al. 2000) and are theoretically capable of regulating insect populations via the control of outbreaks (Godfray and Briggs 1995). Baculoviruses are arthropod specific DNA viruses, characterized by their large proteinaceous occlusion body that protects the virus outside the host (Miller 1997). Infection occurs orally and proceeds through the gut. Infection generally results in death and the transformation of the larva into a liquefied “bag of virus”. rupture of the host cuticle allows occlusion bodies to contaminate plant material or soil. Host range is usually narrow, each baculovirus usually infecting only one genus of Lepidoptera. High pathogenicity and narrow host range make baculoviruses suitable bio-control agents in pest management programs (Moscardi 1999).

Four basic population parameters are fundamental to pathogen fitness (Anderson and May 1981; Cory et al. 1997). These are: transmission, yield (number of infectious stages released from a single host), speed of kill and persistence (the rate of loss of infectious stages from the environment). Host plant effects on persistence and transmission in the field are considered elsewhere (Raymond et al., unpublished data). Infectivity (the probability that disease will result from exposure to a pathogen) is a component of virus transmission and is considered in this paper. The main aims of this study are to understand how variation at the level of the host plant species and at the level of the virus might interact and affect the infectivity of winter moth nucleopolyhedrovirus (NPV), the speed of kill of infected insects and the yield of virus from cadavers. This was investigated using three host plant species (oak, *Quercus robur*; Sitka spruce, *Picea sitchensis*; and heather, *Calluna vulgaris*) and two winter moth nucleopolyhedrovirus isolates. In addition, because the infection process takes place in the midgut of actively feeding larvae and because host plants commonly affect baculovirus infections therein, we formulated the hypothesis that each virus isolate would be adapted to the food plant on which it was collected and thus would have higher fitness when host insects were fed on its plant of origin.

**Materials and methods**

**Virus**

Isolates of *Operophtera brumata* NPV originated from larvae on common oak, *Quercus robur*, at Wytham Wood, near Oxford (Ordnance Survey grid reference SP 463 096) and from larvae on Sitka spruce, *Picea sitchensis*, at Garfwaterhead, near Lanark in the