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TOWARDS GREENER PASTURES - PATHOGENS AND PASTURE PESTS

Summary: Two of New Zealand's most important insect pests, grass grub and porina, are endemic species which have successfully colonised improved pastures. Population densities of these insects within this new environment are far greater than in the native plant systems in which they evolved. Within these high populations diseases have flourished, and high numbers of diseases are recorded from each of these pests. These include bacteria, fungi, nematodes, viruses and protozoa. Diseases have been frequently associated with population collapses in both grass grub and porina, and the role of diseases in natural population regulation is discussed. Insect diseases can also be applied artificially and can have a useful role in pest management.

Keywords: disease; population regulation; biocontrol; grass grub; porina.

Introduction

In the past two centuries the New Zealand environment has changed dramatically under the impact of European colonisation and the establishment of intensive agricultural systems. This massive environmental shift has led to major changes in the abundance of our native fauna. Many previously abundant species have been reduced to low numbers or even extinction, but a few endemic species have managed to bridge the gap between the old and new environments and succeed in the new agricultural conditions. The New Zealand grass grub, *Costelytra zealandica* White, (Coleoptera: Scarabaeidae) and porina (*Wiseana* spp., Lepidoptera: Hepialidae) have been particularly successful in colonising the new ryegrass/clover grasslands which dominate our current agricultural systems.

The grass grub is the only one of more than 100 endemic scarabs (Given, 1952) that has extensively colonised new habitats and become a pest of grasslands in nearly all parts of New Zealand. While several species of *Wiseana* can reach high numbers in pasture there are also a number of non-pest species (Dugdale, 1994).

In improved pastures both species reach densities unknown in the native habitat. Grass grub populations frequently reach more than 500 larvae/m^2 in improved grasslands, while in the native tussock densities are usually no more than one tenth of this number (e.g., Merton, 1980). Similar extremes occur with porina populations.

Insect populations are frequently regulated by density-dependent or delayed-density-dependent factors. If these interactions have evolved under the low densities of insects present in native grasslands it is likely that their actions will be even more extreme in the new environment. In the improved pastures there are few predators and parasites of these insects (Eyles, 1965; Jackson, 1990). Diseases, however, are abundant (Table 1).

Diseases interact with pest populations in either an epizootic or enzootic manner. During an epizootic the frequency of disease in the population increases rapidly to high levels, bringing about a sharp decline in the pest population. Where disease persists in the host population at a lower, more stable level, it is said to be enzootic. Both mechanisms have been implicated in the regulation of pasture pests.

In this paper we will examine the interactions between endemic pests and their diseases in improved pastures, and discuss the role of disease in pest regulation. We will also discuss the artificial application of diseases as a measure for control of pasture pests.

Diseases of grass grub and porina

Bacteria

Grass grub are infected by a number of bacterial diseases, with milky disease and amber disease being the most common. Milky disease is caused by *Bacillus popilliae* Dutky, with two forms occurring in New Zealand (Fowler, 1972, 1974). Type A has a distinctive parasporal crystal within the sporangium while in type B2 the crystal is lacking. Type A is

found throughout New Zealand while type B2 appears to be confined to the lower altitudes in the west of the North Island and the north of the South Island (Jackson, *unpubl. data*). Both types exist as resting spores in the soil and are ingested by the feeding grass grub larvae. Once in the gut, the sporangium breaks, the spore germinates and vegetative cells penetrate to the haemocoel where massive multiplication occurs. As sporulation takes place and the cadaver fills with refractile spores the infected larva takes on the distinctive milky appearance associated with this disease. Upon death of the insect large numbers of spores are released into the soil where they can survive for many years. Milky disease has been recorded as infecting more than 50% of larvae in some populations (Hoy, 1955; East and Wigley, 1985). However, such high levels of disease are more frequently found in the North Island than the South Island.

Amber disease is caused by strains of the bacteria *Serratia entomophila* Grimont *et al.* and *S. proteamaculans* (Paine and Stansfield) Grimont *et al.* which are found throughout the New Zealand pasture environment. These bacteria are also ingested and colonise the gut leading to cessation of feeding and death of the insect (Jackson, Huger and Glare, 1993). Epizootics of amber disease have been recorded with more than 80% of larvae infected (Trought, Jackson and French, 1982). Unlike *B. popilliae, Serratia* spp. are non-sporeformers and their continued survival in the pasture is dependant on at least low numbers of grass grub. There are no known bacterial pathogens of porina.

Viruses

There are few viruses which cause obvious mortality in grass grub. An iridescent virus was found at one site in grass grub larvae (Moore, Kalmakoff and Miles, 1974) and two small Nodaviridae, Flock House virus (FHV: Dearing *et al.,* 1980) and Manawatu virus (MwV: Scotti and Fredericksen, 1987), have been described from a single site (Flock House, near Bulls). In a study in 1980, FHV infections peaked in October at 12.5% of larvae (Wigley and Miln, 1981). MwV was also isolated from Flock House grass grub larvae (Scotti and Fredericksen, 1987). Inapparent viruses in grass grub have also been reported by Hess-Poinar, Jackson and Poinar (1991) and Glare (1992), but little is known about their significance in population decline. However, at the site where the Lake Grasmere virus was found, grass grub populations declined to close to zero in subsequent years (Jackson, *unpubl. data*).

Viruses are more common in porina larvae. An iridescent virus was found to be causing 30% mortality of porina larvae in a heavily-infested grassland at Pelorus Sound in 1969 (Fowler and Robertson, 1972). In advanced infections the virus particles form a crystalline array in the larval fat bodies, producing a blue iridescence. Nuclear polyhedrosis (NPV), granulosis (GV) and entomopox viruses are more frequently found in porina (Moore, Kalmakoff and Miles, 1973). Porina NPV has been the most commonly encountered, and many larvae are infected with more than one type of virus.

Protozoa

Protozoan diseases are common in both grass grub and porina. *Mattesia* sp. (Neogregarina), *Nosema takapauensis* Hall, Oliver and Given, *N. costelytrae* Hall, Oliver and Given, and *Vavraia oncoperae* Milner and Beaton (Microsporida) all infect grass grub. The grass grub protozoa often occur together with the bacterium, *Bacillus popilliae*. Miln (1978) recorded infection levels (due to *Mattesia* sp., *N. takapauensis* and *N. costelytrae*) of up to 90% in the Hawkes Bay region. Generally, *Mattesia* infections occurred in earlier instars than *N. takapauensis*. Mixed infections were common.

Porina are also commonly infected with protozoa, the most obvious being the gregarine *Diplocystis oxycani* Dumbleton. This species forms large cysts in the haemocoel which move freely and are easily visible to the naked eye. These infections do not appear to cause high larval mortality, and the cysts pass through the pupal stage of the host to persist in the adult moths. In 1977 and 1978, 86% and 91% respectively of *W. cervinata* (Walker) moths trapped on the Pahiatua track were infected (Archibald, Pillai and Wigley, 1987). In this way, the adult becomes a dispersal agent for the protozoan, the spores of which are liberated when the moth cadaver breaks down (Dumbleton, 1949).

The microsporidian *V. oncoperae* (Wigley, Malone and Dhana, 1986) is also common in porina and is transmitted transovarially. Infections by this protozoan in porina are considered to be primarily sub-lethal (Wigley *et al.,* 1986).

Fungi

Metarhizium anisopliae (Metschnikoff) Sorokin and *Beauveria* spp. are frequently found as pathogens of both grass grub and porina. These fungi invade the insect haemocoel where hyphae proliferate, killing the insect and producing a hardened cadaver. Fungal spores are produced on the outside of the cadaver. Generally, grass grub larval and pupal deaths due to these fungal pathogens

occur during spring and summer, when soil temperatures are rising. Usually only low numbers of infected larvae are found (e.g., Jackson, 1990), but occasionally epizootics occur, such as those recorded recently by Townsend, Glare and Willoughby (1995). Spring epizootics were found, caused by both *B. bassiana* (Balsamo) Vuillemin and *B. brongniartii* (Saccardo) Petch in Waikato populations of grass grub larvae, resulting in 30-100% mortality.

M. anisopliae was first recorded in porina from a lawn in Nelson, and an epizootic was reported from a Wakanui (Canterbury) pasture in February 1945 (Dumbleton, 1945a). Latch (1965) showed that infection was highly temperature dependent and concluded that the fugus would have little effect in the field, where soil temperatures would be too low during most of the year for its development to be optimal.

Nematodes

Several parasitic nematodes have been isolated from *C. zealandica* (Table 1), however, none of these appear to have a significant effect on grass grub populations.

The nematode *Steinernema feltiae* has been isolated from porina larvae in both the North and South Islands (Kain, Wyeth and Kale, 1981). Infective nematodes enter the insect cadaver, release a symbiotic bacterium which produces a septicaemia killing the insect. Nematodes then develop within the cadaver and eventually produce a new generation of infective juveniles. *S. feltiae* has only been isolated rarely from porina but is known to cause low levels of mortality in some populations.

Natural epizootics and population regulation

While a high number of diseases are found in association with both grass grub and porina in pasture, their role in population dynamics of these pests is harder to determine. A number of diseases have, however, been implicated in population collapses of their hosts (Table 2).

Levels of *Serratia* spp. causing amber disease are generally low in young pastures, but increase following natural outbreaks of grass grub in an apparently delayed-density-dependent manner, leading to a post epizootic decline of the grass grub populations (O'Callaghan, Jackson and Noonan, 1988). Such declines can be predicted. Jackson (1984) found that when the level of disease exceeded 30% in any one year, the grass grub population declined by the following season. Milky disease has also been implicated in grass grub population collapse (East and Wigley, 1985).

Protozoan diseases have been shown to cycle in grass grub populations in permanent pastures in the

Table 1: *Recorded pathogens of the major pasture pests in New Zealand (from Glare, O'Callaghan and Wigley, 1993).*

Pest species	Fungi	Protozoa	Nematodes	Viruses	Bacteria and Rickettsia
Costelytra zealandica (grass grub)	*Beauveria bassiana* *Beauveria brongniartii* *Cordyceps* sp *Fusarium* sp. *Hirsutella stylophora* *Metarhizium anisopliae* *Paecilomyces* sp. *Tolypocladium extinguens*	*Euspora zealandica* *Mattesia* sp. *Nosema costelytrae* *Nosema takapauensis* *Vavraia oncoperae* Unidentified neogregarine *Didymophyes* "odontriae" *Stictospora costelytrae*	*Cephalobellus costelytrae* *Diplogaster* sp. *Mermis* sp. *Psammomermis canterburiensis* *Thelostoma* (?) sp.	Flock House virus Iridescent virus Lake Grasmere virus Manawatu virus	*Bacillus popilliae* *Bacillus sp.* *Micrococcus* sp. *Serratia entomophila* *Serratia proteamaculans* *Rickettsiella* sp.
Wiseana spp. (porina)	*Cordyceps robertsii* *Cordyceps gunnii* *Beauveria bassiana* *Metarhizium anisopliae*	*Vavraia oncoperae* unidentified microsporidan *Mattesia* sp. *Diplocystis oxycani* *Pseudomonocystis spinosus* *Leidyana* "porinae"	*Steinernema feltiae*	Entomopox virus Granulosis virus Iridescent virus Nuclear polyhedrosis virus	

Table 2: *Pathogens associated with population decline of grass grub and porina.*

Host	Pathogen	Reference
Porina	*Wiseana* NPV	Crawford and Kalmakoff, 1977
Grass grub	Protozoan diseases	Miln, 1978
Grass grub	*Bacillus popilliae*	East and Wigley, 1985
Grass grub	*Serratia* spp.	O'Callaghan, *et al*., 1988
Grass grub	*Beauveria* spp	Townsend, *et al*., 1995.

North Island. Protozoan disease levels usually peak between February and July (Miln, 1978, 1982, 1983; East and Wigley, 1985). These diseases have been shown to operate in a delayed-density-dependent manner (Popay, 1992). Barlow *et al*. (1985) estimated that the net effect of protozoan diseases in Taranaki pastures was to reduce grass grub populations by at least 60% of their disease free numbers, but despite this reduction, Popay (1992) considered that protozoan diseases have failed to keep grass grub populations below economic thresholds.

Porina outbreaks frequently occur in young pastures and can be followed by epizootics of virus through the population. At the height of epizootics many larvae may be infected and dead larvae can be collected from the ground surface (Crawford and Kalmakoff, 1977). Epizootics are more likely to occur in young pastures, with up to 80% of larvae infected, than in older pastures where infection levels seldom exceeded 10% (Moore *et al.,* 1973). This led to the hypothesis that new pastures are initially virus-free, which allows porina populations to increase in the absence of disease and reach damaging densities. Low virus levels were attributed to ploughing which removed virus inoculum from the soil, either by deeply burying it, or by exposing it to ultra-violet light (Crawford and Kalmakoff, 1977; Kalmakoff, 1979; Fleming *et al.,* 1982). As a pasture ages, virus levels increase until an epizootic occurs, rapidly reducing the porina population. After this event, the virus and host exist together at more stable levels; porina populations are relatively low and the disease is enzootic in the population. On re-examining this hypothesis and the data on which it was based, Barlow, French and Pearson (1986) suggested that the virus incidence in three of the four pastures studied was as much a function of the year as the age of the pasture, questioning the impact of virus in population regulation. However Barlow's challenge to the hypothesis does not provide an alternative explanation for the original data of Moore *et al*. (1973). Despite the reservations outlined above, it is clear from the available data that viral infection rate increases in a delayed-density-dependent manner, resulting in high levels of disease in the later stages of a porina outbreak. It is also evident that porina outbreaks were only recorded in pastures with low levels of virus.

It appears from studies of larvae infected with NPV in the field (Fleming *et al.,* 1986) that the course of infection is extremely slow when compared with other NPVs, with larvae becoming infected at early instars, but not developing full symptoms until some months later. If so, this is a very unusual baculovirus/host system, and further laboratory studies could greatly enhance our knowledge of how these viruses have evolved to suit the life cycles of their hosts.

Application of pathogens for pest control

During the last 5 years, *S. entomophila* under the trade name Invade, has been applied to more than 10 000 ha of pasture. Application generally results in 15-20% infection in the first 4-8 weeks which is independent of the density of the host, resulting in a 40-50% reduction in the total population in the season of application (Jackson *et al.,* 1992). In subsequent seasons, disease persists in the pasture showing a delayed-density-dependent relationship with the host population similar to that in natural epizootiotics (Jackson, 1993).

Small scale field trials applying *B. popilliae* to grass grub populations have been attempted in New Zealand but with little success (Dumbleton, 1945b; Kelsey, 1967).

The fungi *Beauveria* and *Metarhizium* can be easily cultured on grains or simple media, so these fungi have been tested in the field for many years. *M. anisopliae* was considered as a biocontrol agent of grass grub by Latch (1965), but due to temperature limitations, the fungus was thought to be unlikely to be effective. However, a low-temperature-active strain of *M. anisopliae* has recently been isolated in New Zealand (Glare, Townsend and Young, 1994). Field trials using *Beauveria* spp. and *M. anisopliae* for grass grub control are currently in progress in both the North and South Islands (Glare, Townsend and Willoughby, *unpubl. data*).

Field trials using a chipped wheat bait inoculated with *M. anisopliae* against porina have been quite successful, but again soil temperature was a limiting factor (Latch and Kain, 1983). At a mean maximum soil temperature of 17°C, an infection rate of 80% was achieved.

Tests with *Bacillus popilliae*, protozoa and viruses have been limited by the lack of *in vitro* methods of production for these organisms

Management of diseases

Application of diseases may not be necessary to manage pest populations if they can be managed *in situ*. This approach has been suggested for the management of porina using the natural incidence of NPV. Kalmakoff (1980) made seven recommendations for pasture management practices to maintain NPV, including direct-drilling porina-damaged pastures rather than cultivating, intensive rotational stocking to distribute virus, and the use of older rather than younger pastures for hay production, because long grass and lack of stock was believed to favour porina larval survival. However, when tested experimentally (Kalmakoff *et al.,* 1993), these practices had no significant effect on the prevalence of NPV in the porina populations. Nevertheless, it was shown that ploughing did remove NPV from pasture, as predicted, and that the virus infection rate rapidly increased to reach the same levels as found in control plots within three years.

Jackson (1993) also recommended the maintenance of mature pastures to preserve grass grub pathogens and proposed the idea of pathogen-enhanced integrated pest management systems for the management of grass grub.

Discussion

The presence of these two endemic pest species at high levels in pastures allows some generalisations to be made about diseases. Firstly, where insect populations build to high levels over a number of years, diseases will become increasingly abundant in the later populations. The key question is whether these diseases do, in fact, regulate the populations. Population analysis has shown that most diseases operate in a delayed-density-dependent manner. At low populations, i.e., in new pastures or after weather-induced population collapse, there will be little evidence of disease. As the population increases disease will enter the population and often multiply to epizootic proportions. The cases of grass grub and porina show that many diseases can fill this niche and the species that eventually dominates will be dependent on region, climate and existing innoculum. In some cases multiple diseases will occur. As the epizootic spreads, the host population density will decrease. This pattern has been shown for grass grub with *Serratia,* milky disease, protozoa and fungi, and for porina with viruses. In the post collapse pastures, pest populations have been observed to remain at low levels for some years, but the role of disease in keeping levels low is harder to determine, as the debate over enzootic control of porina by virus indicates.

Application of *Serratia entomophila* as a cultured inoculum has shown that epizootics can be initiated artificially and bring about control of grass grub. This approach has merit for other pests, but is limited at present by the number of organisms that can be cultured in sufficient numbers for application.

Thus, it appears that porina and grass grub, having been released from constraints to population growth imposed by their native habitat, have provided an ideal environment for multiplication of diseases. High population densities provide the ideal situation for transmission of microbes, as is evidenced by the frequency of epizootics of disease among populations of grass grub and porina. Diseases, therefore are an important resource for management of these pests in the future.

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