The impact of invertebrate pests on pasture persistence and their interrelationship with biotic and abiotic factors

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Abstract
New Zealand pastures are host to a range of native and exotic invertebrates. Many of these are pests that feed on the sown plant species, often causing plant death and deterioration in the productivity and persistence of the sward. While most research has focused on pest biology and control, studies of plant productivity show dramatic acute (short-medium term) and chronic (long-term) effects. For example, grass grub has been reported to cause 50% losses to ryegrass swards and Argentine stem weevil can cause a 20% loss of productivity, but the long term effects through loss of the sown species and changes in composition can be even more severe. Insect damage can be exacerbated by other biotic (e.g. weed invasion, grazing animals, plant pathogens) or abiotic factors (e.g. climate, soil fertility) to further reduce plant persistence. Some biotic and abiotic factors may interact with insect pests to have positive effects on pasture persistence, e.g. biocontrol agents that reduce pest density or addition of fertiliser to enable plants to recover from insect damage. For many pasture pests, knowledge of their ecology is based on research from over 20 years ago that, while still valid, needs to be updated to account for modern intensive pasture management practices, such as intensive grazing with a lack of reseeding, and new cultivars. To improve pasture persistence, integrated research programmes are needed that examine the relative importance of all factors contributing to plant survival and develop strategies to mitigate their effects.
Keywords: Argentine stem weevil, black beetle, clover root weevil, drought, grass grub, grazing pressure, manuka beetle, nematodes, pasture persistence, pasture quality, pasture yield, porina, soil fertility, striped chafer.

Introduction
The New Zealand pasture system of exotic grasses and clovers has been the mainstay of the New Zealand economy for more than a century but is susceptible to a wide range of invertebrate pests, weeds and pathogens. These can occur at extremely high population densities that reduce the economic viability of the system (Barlow & Goldson 2002). The direct effects of acute pest outbreaks, resulting in visible damage and plant death, can be dramatic but are often spatially and temporally patchy with pastures appearing to recover through the ingress of colonising plant species from the seed bank in the soil (e.g. Tozer *et al.* 2010). However, chronic pest infestation is also important, with more insidious effects on pasture persistence. The balance of these pests may alter from season to season due to climatic effects and pasture management practices. In the long term, pest infestations, interacting with biotic (e.g. weeds, grazing animals) and abiotic (e.g. soil moisture, temperature and fertility) factors, can be responsible for plant mortality and a reduction in sown species density. These changes in pasture composition are followed by a decline in sward productivity, deterioration in forage quality and reduced sustainability of pastoral farms. Not all pest infestations result in plant mortality. In particular, sucking insects (e.g. mealybugs and aphids) contribute to reduced plant vigour and decreased pasture production (Pennell *et al.* 2005), but may not result in plant death.

New Zealand has a long history in pasture entomology and pest management but this has mostly focused on the pest biology and short term impacts. In this paper we review historical data on pasture damage caused by key nationwide pest species (grass grub, clover root weevil, nematodes, porina and Argentine stem weevil) and examples of pests with severe regional and sporadic impacts (black beetle, manuka beetle and striped chafer). Pest impact will be considered in terms of sown species survival as well as longer-term pasture persistence and sustainability. Interactions with other biotic and abiotic factors in the pasture ecosystem will be discussed and areas highlighted where there are important knowledge gaps.

Review of pasture damage by key insect pests in New Zealand

Grass grub

The New Zealand grass grub (*Costelytra zealandica*) (White) (Coleoptera: Scarabaeidae: Melolonthinae) is a ubiquitous, endemic insect pest that damages pasture through larval feeding on the roots of pasture grasses and clover. In grass grub-prone areas there is a steady and predictable increase in population after sowing new pastures (East & Kain 1982). Larvae usually reach damaging levels 2-4 years from sowing (e.g. East *et al.* 1979, Fraser 1994) and their impact can be observed as damage patches that increase in size from year to year (Kain 1975), resulting in lost production. East *et al.* (1979) showed that grass grub populations of more than 200/m^2 in 3-year-old pastures on the pumice country of the North Island caused losses of 11-44% of the grass component in mixed ryegrass/white clover swards in the year of attack and as much as 49% loss to pure ryegrass swards. Substantial losses of dry matter production of sown pasture species were also demonstrated by Kain *et al.* (1979) when new pasture was established on grass grub infested soil in Hawke's Bay. While damage is acute from direct feeding, long-term yield and quality losses also result from changes in sward composition. In dryland farming, Kain & Atkinson (1972) showed that weed ingress following grass grub attack is common, and Fraser (1994) commented that ryegrass-based pastures in Canterbury are frequently ploughed up after 4 years due to grass grub damage. Nearly 20 years ago, Garnham & Barlow (1993) estimated that grass grub in New Zealand caused over $40 M per annum in reduced stock carrying capacity and costs of renovation.

After plants have been damaged by root feeding, pasture repair is practised by some farmers through stock treading (East & Pottinger 1983) and heavy rolling (Stewart *et al*. 1988). However, new plants of the sown genotype can only be regenerated in bare patches through germination from the seedbank (L'Huillier & Aislabie 1988), a process that is not encouraged under modern pasture management systems. Assessment of grass grub impact on the sown species is further confounded by the build-up of diseases in high density populations (Jackson *et al.* 1999). This will lead to a natural decline in the grass grub population which, together with "apparent pasture recovery" led by invasive plant species, can mean the impact of this pest on the original sown cultivar(s) is underestimated.

Clover root weevil

Clover root weevil (CRW), *Sitona lepidus* Gyllenhal (Coleoptera: Curculionidae), is a recent arrival and has yet to establish in many South Island districts (Phillips *et al.* 2010). It can go through an initial boom and bust cycle on arrival at a new site, with associated severe clover loss, recovering to relatively stable larval populations and lower mean annual clover levels thereafter (Gerard *et al.* 2009). The weevil attacks clovers only; white clover is more susceptible than other clovers, particularly when under moisture stress (Crush *et al.* 2008). While adult weevils can cause severe seedling losses and therefore poor regeneration from the seed bank, it is the larvae that have greatest impact on clover persistence. With two overlapping larval generations, feeding damage to nodules, roots and stolons occurs year round. Plant resources are directed below ground to replace nodules and roots, resulting in reduced foliage production (Gerard *et al.* 2007). As well as these direct impacts on clover persistence, CRW damage affects clover in other ways. For example, in spring, when combined with the increased availability of nitrogen in the root zone from damaged roots and insect frass (Murray & Hatch 1994), pasture grasses will shade and outcompete clovers. Clover is also particularly vulnerable when CRW damage is combined with other biotic and abiotic factors, such as heat stress to stolons in summer and grazing pressure throughout the year.

A parasitoid wasp (*Microctonus aethiopoides* Loan (Hymenoptera: Braconidae)) imported from Ireland is effective as a biocontrol agent (Gerard *et al.* 2010). Clover-friendly pasture management practices are recommended to maintain the stability of the biocontrol system and minimise the loss of clover in pastures infested with CRW. These include preventing pastures becoming rank in spring, leaving some cover in summer, and applying frequent low rates of nitrogen fertiliser (Eerens *et al.* 2005).

Nematodes

Plant parasitic nematodes affect establishment and persistence of New Zealand pastures, particularly the clover portion. The root knot (*Meloidogyne* spp.) and cyst (*Heterodera* sp.) genera of nematodes are the most damaging to clover, with two species of root knot (*M. trifoliophila* and *M. hapla*) and a single species of cyst nematode (*H. trifolii*) predominant in New Zealand pastures. While both genera are found in many North Island pastures, in South Island pastures it is more common to find only cyst nematodes (Mercer & Woodfield 1986; Skipp & Christensen 1983). The impacts of nematodes and research to mitigate their effects on pasture production and persistence have been reviewed by Mercer *et al.* (2008). Plant damage is caused by disruption of root function, including nitrogen fixation. A region-wide series of plots of pasture swards chemically treated to remove nematodes showed increases in clover yield of 40% and in nitrogen fixation of 55% (Watson *et al.* 1985) and similar results have been found in other field and glasshouse studies around New Zealand (see Mercer *et al.* 2008).

Abiotic factors that impact on nematode damage include soil temperature, with yield loss increasing with increasing temperature (see Mercer *et al.* 2008; N.L. Bell, AgResearch, unpublished data), and soil moisture, which interacts with soil temperature to exacerbate damage (N.L. Bell, AgResearch, unpublished data). Of biotic factors influencing damage to clovers, traditional plant breeding has been used to develop nematode-resistant or -tolerant plants (Mercer *et al.* 2008) and these will improve clover productivity and persistence in nematode-infested pastures once released as commercial cultivars. There are also a number of microbes that may have an impact on nematode populations (Hay & Skipp 1993) in established pastures although there has been little research to quantify this.

Porina

Porina is a complex of several species of *Wiseana* (Lepidoptera: Hepialidae), all of which have one generation per year. The larvae live in burrows in the soil and feed on the foliage of ryegrass, white clover and many other pasture plants. Porina is a denuding rather than a grazing pest, which means that leaves and tillers may be severed at ground level and growing points damaged irretrievably (Barlow 1985a). Even at low larval densities, porina altered the composition of pasture by selective grazing (Farrell *et al.* 1974). French (1973) calculated that 20-40 larvae/m^2 consumed the equivalent foliage of a ewe with lamb, while Barlow (1985b) estimated that at a density of 100 larvae/m^2, stocking rate would need to be reduced by 5 ewes/ha. Stewart & Ferguson (1992) showed that reducing populations by 30 larvae/m^2 and 65 larvae/m^2 provided an extra 1100 kg DM/ha both in spring and early summer. Usually 20-40 larvae/m^2 is considered indicative of the point at which losses in pasture productivity will be incurred, with greater densities leading to the destruction of sown species and their replacement by less productive weeds. A density of 141 larvae/m^2 completely removed white clover and grass from areas of infested pasture (Stewart & Ferguson 1989). Occasionally populations of >330 larvae/m^2 are encountered and in this situation whole paddocks become devoid of any sown pasture species (C.M. Ferguson, AgResearch, unpublished data).

In porina-prone areas, outbreaks can be predicted to some extent. The precursor to high porina numbers is a disruption of naturally occurring pathogens that normally regulate porina numbers (Crawford & Kalmakoff 1977). This can be caused by climatic factors, such as dry summers, but the main disruption is cultivation. Between 2 and 4 years (most often in the third winter) after the disruption, porina numbers reach damaging levels and there is a significant impact on pasture production and composition. Subsequently the porina-pathogen association is re-established, porina numbers reduce and damage becomes more insidious. However, by this time pasture production reductions have occurred and when porina populations are high, significant and irreversible losses of pasture plants have taken place.

Argentine stem weevil

Argentine stem weevil (ASW), *Listronotus bonariensis* (Kuschel) (Coleoptera: Curculionidae), was recognised as one of New Zealand's most damaging pests of pasture (Prestidge *et al*. 1991), causing total herbage production losses of up to 18% (Prestidge *et al*. 1984) and major impacts on seasonal yield of pasture and animal production systems (Barker & Baars 1988), until the implementation of biocontrol in the 1990s (McNeill *et al.* 2002). ASW is a pest of numerous graminaceous crops including most pasture grasses, of which annual species such as *Poa* spp. tend to be more favourable hosts than perennials (Barker 1989). Adult feeding is characterised by windowing of the leaves (Barker *et al*. 1981) and seedling plants can be killed (Trought 1976; Prestidge *et al.* 1994), but larval mining of the stem causes the greatest pasture yield losses (Hunt 1990; Barker *et al*. 1989). Damage can be manifest as reduced vigour or death of plants, while stock feeding on weakened plants can also cause 'pulling' (e.g. Prestidge *et al.* 1989).

Management of ASW in perennial ryegrass was initially based solely on the mutualistic association between ryegrass and the endophytic fungus *Neotyphodium lolii* (Prestidge & Ball 1995). ASW causes changes in pasture composition through selectively ovipositing on nil-endophyte ryegrass tillers. The subsequent larval feeding reduces persistence of nil-endophyte plants and causes a rapid change to high endophyte ryegrass populations (Francis & Baird 1989; Prestidge *et al.* 1984; Hume & Brock 1997). Studies in the central Volcanic Plateau recorded increases in endophyte levels in Nui by 25-400% after just 1 year (Prestidge *et al.* 1984), indicating that ASW has a dramatic effect on persistence of individual plants. The efficacy of novel endophyte strains in ryegrass against ASW has been summarised in this volume (Popay & Hume 2011). Biocontrol by the parasitoid *Microctonus hyperodae* has significantly reduced ASW adult numbers (Goldson *et al.* 1998; Barker & Addison 2006), and has been helpful in reducing reversion from low to high endophyte as well as for improving persistence of both endophytic and non-endophytic pastures (McNeill *et al*. 2001).

ASW has not been considered a significant pest of established pasture in Otago and Southland, which was attributed to low temperatures precluding more than one complete generation (Ferguson *et al.* 1996). This meant that generally ASW densities were low (0-132 weevils/m^2) (Ferguson *et al.* 1994) relative to other areas of New Zealand and farmers were able to utilise endophyte-free ryegrasses. However, in the last decade much higher weevil densities have been found in the southern South Island (up to 600 weevils/m^2; C.M. Ferguson, AgResearch, unpublished data), and this has coincided with the rapid increase in dairying in the region. The impact of the weevil in these dairy pastures has not been measured, but is likely to be considerably greater than previously thought.

Sporadic and regional pests

The pests discussed in the previous section are either widespread throughout New Zealand or inflict damage to pastures on an annual basis. In this section, three pests that are currently localised to specific regions in New Zealand are briefly described. While distribution of these pests is currently restricted, the damage they cause can be extremely severe, with major impacts on pasture persistence. There are a number of other pests that cause regional, sporadic or chronic damage to pastures, including clover flea (*Sminthurus viridis* (L.) (Collembola: Sminthuridae); also known as lucerne flea), black field cricket (*Teleogryllus commodus* (Orthoptera: Gryllidae)), redheaded cockchafer (*Adoryphorus couloni* (Burmeister) (Coleoptera: Scarabaeidae)), Tasmanian grass grub (*Aphodius tasmaniae* Hope (Coleoptera: Scarabaeidae)), pasture mealybug (*Balanococcus poae* (Maskell) (Hemiptera: Pseudococcidae)), root aphid (*Aploneura lentisci* (Pass.) (Hemiptera: Aphididae)) and slugs (Gastropoda), but these are not discussed in detail in this paper.

Black beetle (*Heteronychus arator* (F.) (Coleoptera: Scarabaeidae)

The pasture production effects, damage thresholds and interactions with some biotic and abiotic factors of black beetle are reviewed elsewhere in this volume (Bell *et al.* 2011). Warm spring temperatures appear to be critical for the establishment and survival of early instar larvae, which will lead to the damaging populations of the mature root-feeding larvae in summer. If larval populations are high in February, damage is likely to be exacerbated by drought. While some fungal endophytes protect grasses by reducing adult beetle feeding and thereby egg-laying and subsequent larval populations, the presence of C_4 weed grasses (e.g. paspalum) in pastures is likely to help sustain high beetle populations.

Manuka beetle

Manuka beetles (*Pyronota* spp. (Coleoptera: Scarabaeidae)) have traditionally been considered as significant pests only in areas close to manuka bush (Thomson *et al.* 1979), but damage may have been underestimated as the larvae are frequently mistaken for "small" grass grub. Large-scale land modification through flipping (inversion of the soil profile) on the West Coast has induced a major outbreak of two species of manuka beetles, *P. festiva* and *P. setosa* (Townsend *et al.* 2010). In uncontrolled conditions, populations of both species have risen to high levels (>1100 larvae/m^2) completely destroying the ryegrass/clover pastures within 2-3 years of sowing. With increasing intensification of pasture production in previously marginal areas, manuka beetles are likely to become a greater problem in the future.

Striped chafer

Striped chafer (*Odontria striata* (White) (Coleoptera: Scarabaeidae)) can be a significant pest in developed tussock grassland, whether oversown or cultivated from tussock at mid-altitude (400-600 m). It is rarely a problem in low-altitude intensively grazed pasture. The biology and phenology in Otago has been described (Barratt & Campbell 1982; Barratt 1982). The species is relatively mobile in the larval stages, and tends to cause damage more evenly across the pasture compared with the patchy damage typical of grass grub. Densities can reach 200-300/m^2 and control with pesticides applied in spring was shown to provide up to 40% increases in dry matter production (Barratt & Lauren 1984). Little is known about the impacts of this species on pasture persistence, but farmers in affected areas have noted ingress of Californian thistle into pastures with a history of striped chafer infestations (Barratt & Brash 1985).

Discussion

The studies reported above show that insect pests and nematodes can cause significant losses of sown species in pastures leading to deterioration in pasture quality and productivity. In the following discussion, the complex interactions between pests and other components of the pasture ecosystem will be considered. At the height of a severe pest attack the cause of pasture loss is usually obvious, but it is more difficult to determine the effects of chronic, low-level insect feeding or attribute the cause of pasture deterioration once the feeding stage is completed or the insects have left the pasture.

While it is clear that invertebrate pests are detrimental to pasture plant persistence, how their impacts are modified by their interactions with other biotic and abiotic factors in the pasture ecosystem is poorly understood. Once sown, pastures are a dynamic system and the interactions between component species will cause shifts in diversity and abundance of species over time (e.g. Brown & Gange 1992). For example, clover flea can significantly alter species composition in developing grassland communities but interactions with other collembolan and plant species profoundly modify clover flea impacts (Barker 2006). Shifts in plant diversity induced by pests will also cause shifts in invertebrate density. Thus, under attack from invertebrate pests, preferred plant hosts fail to persist and this causes a subsequent decline in pest populations. From a survey of 40 farms, Prestidge *et al.* (1984) found that as susceptible ryegrasses were killed, the Argentine stem weevil populations responsible also fell, and the remaining ryegrasses were those protected by the endophytic fungus *Neotyphodium lolii*. Similar situations have been recorded for CRW, nematodes and grass grub.

Insect pests usually occur in multi-species complexes, and their impacts may be additive, i.e., damage by one pest adds to or increases susceptibility to damage from another. For example, in a pasture species trial, King *et al.* (1982) found that black beetle decreased the ryegrass component and white fringed weevil (*Graphognathus leucoloma*) reduced clover yield. Another example of this type of biotic interaction is that the stress response by plants to root loss can improve food quality for above-ground pests like aphids (Masters *et al.* 1993), which in turn are vectors of plant viruses (e.g., Mohamed 1978). However, in some situations, damage by one pest may render plants an unsuitable food resource for another. For example, larval feeding by CRW can induce production of defence compounds in some red clovers (Gerard *et al.* 2005). Also, pests compete for the same food resource, so it will not be possible to simply add up damage estimates for individual pests to arrive at a likely total pest damage estimate. A small plot trial by Gerard *et al.* (2007) showed a highly significant inverse relationship between numbers of grass grub larvae in autumn and CRW larvae the previous spring, and that more clover feeding nematodes were found in plots with low CRW larval populations.

Grazing animals can influence the impact of insect pests on pasture, and responses of different pest species to grazing have been described by East & Pottinger (1983). The type of farm system can also have a marked influence on susceptibility to pests. For example, Skipp & Lambert (1984) found cattle-grazed pasture suffered greater damage from insect and slugs than sheep-grazed pasture, while clover flea has been shown to be most pronounced on dairy farms (Wrenn *et al.* 1983).

It is sometimes difficult to separate out direct cause and effect of biotic factors from associated changes in pasture persistence. For example, Rath & Rowe (1993) found that an uncontrolled population of the root-feeding redheaded cockchafer larvae caused a 43% loss of perennial ryegrass in autumn pastures, followed by ingress of *Poa anua*, flatweeds and thistles in the following spring. Weed ingress following grass grub damage has been reported by Fenemore (1966), Kain (1975) and French *et al.* (1983). In these cases, the authors attributed the loss in pasture persistence to insect pest damage, with colonisation of bare ground by weeds following as a secondary effect. However, there are other situations where weeds have been shown to have a direct effect on pasture plant persistence. For example, Wardle *et al.* (1998) described how the weed nodding thistle (*Carduus nutans*) had a significant impact on growth and persistence of pasture plants, while Wardle *et al.* (1995) showed that the presence of ragwort (*Senecio jacobaea*) was associated with increased perennial ryegrass but decreased white clover. Regardless of the mechanism, the replacement of sown pasture species with other plants will directly affect the potential production from the pasture.

Abiotic factors also interact with pests to influence damage. For example, Sanderson *et al.* (2003) found that insect damage to white clover in pastures in the north-eastern USA was much more severe in drought years than those with favourable rainfall. This could mean that damage from root-feeding pests may affect the uptake of nutrients and the effects can be mitigated by supplying additional fertiliser (e.g. Prestidge & East 1984).

Dry matter production from pastures is notoriously variable within a range of time scales from months to years. Even within intensively-managed dairy farms in the Waikato, the best paddocks outperformed the worst by 30 to 122% more DM/ha/year and there was little relationship between years in paddock yield (Clarke *et al.* 2010). The contribution of cumulative damage by multiple pest species over time to these variations in yield is poorly understood. Because of the interactions with biotic and abiotic factors, the true impact of pests is frequently overlooked. While acute damage is well recognised by researchers and farmers and is a common reason for pasture renovation, the contribution of chronic pest damage to loss of sown species and declining pasture productivity has not been studied in detail in modern pastures.

A critical aspect of interpreting variable, and particularly declining, levels of pasture production is understanding the effect of pests on individual plant survival. However, a key challenge in the assessment of the effects of pests on pasture plant persistence is the lifecycles and mobility of the pests. At the point when damage becomes apparent, the causative pest may have developed to a new less-visible lifestage (e.g. pupae or eggs) or moved to a new location. In addition, many damaging pest species are cryptic or subterranean, so are not readily observed. Damage to roots makes the plant highly vulnerable to biotic and abiotic factors, such as pulling during grazing or drought, with subsequent impacts on plant persistence. This challenge is even more extreme for microscopic pests such as nematodes.

It is essential that future research programmes are fully integrated so they consider all biotic and abiotic factors affecting pasture persistence. This includes incorporating adequate pest assessment to lessen the knowledge gaps outlined above and provide targets for ameliorating the impacts of these pests on pasture persistence.

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