BioControl (2013) 58:149–162
DOI 10.1007/s10526-012-9480-0

REVIEW

Potential effects of climate change on biological control systems: case studies from New Zealand

P. J. Gerard · J. R. F. Barringer · J. G. Charles · S. V. Fowler · J. M. Kean · C. B. Phillips · A. B. Tait · G. P. Walker

Received: 19 January 2012 / Accepted: 1 August 2012 / Published online: 21 August 2012

Abstract Biological control systems are integral to New Zealand's success as a nation reliant on exporting quality agricultural, forestry and horticultural products. The likely impacts of climate change projections to 2090 on one weed and four invertebrate management systems in differing production sectors were investigated, and it was concluded that most natural enemies will track the changing distributions of their hosts. The key climate change challenges identified were: disparities in natural enemy capability to change distribution, lack of frosts leading to emergence of new pests and additional pest generations, non-target impacts from range and temperature changes, increased disruptions caused by extreme weather events, disruption of host-natural enemy synchrony, and insufficient genetic diversity to allow evolutionary adaptation. Five classical biological control systems based on the introduced species *Longitarsus jacobaeae*, *Cotesia kazak*, *Aphelinus mali*, *Microctonus aethiopoides* and *Microctonus hyperodae* are discussed in more detail.

Keywords Climate change · Biological control · *Longitarsus jacobaeae* · *Cotesia kazak* · *Aphelinus mali* · *Microctonus* spp.

Handling Editor: Dirk Babendreier

P. J. Gerard (✉)
AgResearch, Ruakura Research Centre, Private Bag 3123,
Hamilton 3240, New Zealand
e-mail: pip.gerard@agresearch.co.nz

J. R. F. Barringer · S. V. Fowler
Landcare Research, PO Box 40, Lincoln 8140,
New Zealand

J. G. Charles · J. M. Kean · G. P. Walker
Plant & Food Research Limited, Private Bag 92169,
Auckland 1142, New Zealand

C. B. Phillips
AgResearch, PO Box 60, Linn 8140, New Zealand

A. B. Tait
National Institute of Water and Atmospheric Research,
Private Bag 14901, Wellington, New Zealand

Introduction

Climate change has generated considerable discussion and research into possible effects on agroecosystems (Fuhrer 2003). As the location, nature and productivity of agricultural and natural environments change, so will the composition, distribution and phenology of the beneficial invertebrates that safeguard their productivity and sustainability (Cock et al. 2011). Most studies of the impacts of climate change focus on individual species, whereas biological control systems involve interactions between species at different trophic levels.

Berg et al. (2010) analysed published literature for two traits that impact on a species dealing with climate change: thermal sensitivity and dispersal ability. They found pronounced differences among trophic groups e.g. species living in soil, have a weaker thermal response traits compared with those above ground. They emphasised that temperature-induced mismatch in development could result with serious consequences.

Under climate change, the effectiveness of some biological control agents (BCAs) may change. Stireman et al. (2005) predicted that the frequency and intensity of pest outbreaks will increase as climate becomes more variable and disrupts the stability of existing biological control systems. Reviews by Hance et al. (2007) and Thomson et al. (2010) summarise ways that climate change is likely to influence natural enemies of agricultural pests. Here, we analyse potential impacts on biological control systems in New Zealand (NZ).

NZ is long narrow country stretching over 1,600 km between 34° and 47° South. It consists of two main islands (North and South), and a number of smaller islands. The climate varies from warm subtropical in the far north to cool temperate in the far south, with severe alpine conditions in the mountainous areas. The mountain chains along its length block the prevailing westerly winds, dividing the country into dramatically different climate regions. The West Coast of the South Island is the wettest area (2,000–10,000 mm rainfall per year), whereas just over 100 km away, the plains to the east are the driest with some districts averaging below 400 mm/year^{-1}.

NZ's latitudinal range, diversity of climates and relative lack of biodiversity in its mostly European species-based agricultural ecosystems makes it an ideal place in which to examine the effects of climate change on biological control systems. Species innocuous in their natural range have become pest and weed problems in the absence of their co-evolved BCAs. Conversely, classical biocontrol systems are very successful (Ferguson et al. 2007). BCAs have become a principal means of pest control in NZ's agricultural systems and are integral in the successful integrated pest management (IPM) programmes of the largest export crops such as kiwifruit and pipfruit. NZ is ranked fourth after USA, Australia and Canada for number of classical BCA introductions (Cock et al. 2010).

Here, we review the possible impacts of climate change on biological control systems in NZ, and present five illustrative case studies from a range of weed and pest biocontrol systems. While most relevant to NZ, the results are applicable to biological control systems in other temperate countries.

Climate projections for New Zealand

The climate change scenarios and data used for all analyses in this study had the following characteristics (see Mullan et al. 2008 for more details):

- *Projected years:* base 1990 (average observed from 1980 to 1999), 2040 (average projection for 2030–2049), 2090 (average projection for 2080–2099).
- *Carbon emission scenarios:* 4th Assessment Report of the Intergovernmental Panel on Climate Change scenarios A1B (medium emissions) and A2 (high emissions).
- *Global climate models* (GCMs): the prediction for NZ's future climates were based on 12 GCMs that best fitted NZ, based on validation against the observed climates of the 20th century.
- *Clim variables:* mean monthly temperature expressed as a mean anomaly from the base period, mean monthly rainfall as a percentage of that of the base period. Relative humidity is likely to be very similar to current values, though absolute humidity may differ.
- *Spatial resolution:* large-scale model predictions were statistically down-scaled to a 0.05° latitude/longitude resolution grid based on the NZ Geodetic Datum projection (approximately 5 km resolution).

The Mullan et al. (2008) 12-model average A1B scenario projected that temperatures would increase by about 1 °C by 2040, and 2 °C by 2090, with the changes most pronounced in the north of the South Island, and the North Island. Westerly winds will strengthen in winter and spring and decrease in summer and autumn, resulting in changes in rainfall patterns. For 2040 the changes in annual precipitation ranged from an increase of 7.5 % (west coast of the South Island) to a decrease of 5 % (along the eastern regions from the central South Island north to the upper North Island, and around up to Northland, the northernmost region in NZ), relative to 1990. For 2090 the projected changes in annual precipitation range from an increase of over 10 % (west coast of the South Island) to a decrease of 7.5 % (along the eastern coastal strip from the central South Island north to the upper North Island, and in Northland), relative to 1990.

Extreme rainfall events may occur about twice as often by 2090 under an A1B scenario and three to four times as often under an A2 scenario. Severe droughts are projected to occur at least twice to four times as frequently in drought-prone regions. As warmer air holds more moisture, there could also be increased winter snowfalls to low elevations in some regions, although the duration of seasonal snow lying on the ground would be shortened.

Likely challenges arising from climate change on NZ biological control systems

International literature on the effects of climate change on invertebrates was reviewed and circulated amongst NZ biological control specialists. A workshop was held where their specific opinion and analysis was sought on the likely impacts of climate change on major NZ biological control systems. Five illustrative case studies were then selected for more detailed investigation.

Climate change effects on a biological control system may manifest at different scales from geographic distributions to evolutionary changes in natural enemy populations. Summarised below are the six key challenges to maintaining biological control under climate change identified by the contributors.

Species distributions

The crops and forages produced in a region will change as growers choose those that optimise economic returns in the prevailing climate and markets. As climate change is a gradual process, it is predicted that pests and their BCAs will move with the host plants. Increased temperatures will extend the southern range of cold-limited species and increase the altitude at which they can survive. A 2 °C rise in temperature from 1990 to 2090 is equivalent to a shift of current northern hemisphere conditions of 600 km latitude or 330 m in elevation (Parry 1989). As this approximates to 6 km per year latitude or 3.3 m per year elevation, most invertebrates would be capable of tracking such changes. However, managed releases may be necessary for some BCAs with low dispersal rates. In addition, the time taken for biological control systems to integrate into a new area may be influenced by availability of nutritional resources and overwintering or aestivation sites.

The expectation that everything will move south will be modified by disparities in the climate tolerances of hosts and their BCAs. Diapause, which allows populations to survive winter conditions, is often induced by photoperiod rather than temperature, while temperature plays a more important role in aestivation (Tauber and Tauber 1976). Because of NZ's mild climate, the ranges of some continental species already extend beyond their native latitudinal limits [e.g. *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae)]. Therefore further geographical shifts in latitude and associated seasonal photoperiods may impact on host-parasitoid relationships in unpredictable ways.

Milder winters and longer growing seasons

Milder winters will allow both increased use of subtropical species in NZ production systems and establishment of new pests and weeds. NZ has been exposed to airborne species from Australia for millennia, but most frost-sensitive species have not established (Phillips et al. 2006). Without co-evolved BCAs, some invaders will become pests, while others, such as hyperparasitoids, may disrupt existing biological control systems.

Longer growing seasons may allow species like aphids and thrips to multiply too rapidly for their BCAs to keep pace. In addition, there are "sleeper pests", species already in the country which are kept in check by factors such as host unavailability and cold. For example, a rare outbreak of tropical armyworm *Spodoptera litura* (F.) (Lepidoptera: Noctuidae) occurred in autumn 2011 when above average temperatures allowed an extra generation to develop (Gerard et al. 2011). Other minor pests persisting in isolated microhabitats or regularly arriving from Australia by wind [e.g. tropical grass webworm *Herpetogramma licarsisalis* (Walker) (Lepidoptera: Crambidae) (Dymock et al. 2009)] may also increase in significance.

There is potential for pre-emptive action against sleeper pests, particularly if biological control has already been successful overseas. The successful biological control of mist flower *Ageratina riparia*, (Asteraceae) in NZ provides an example (Barton et al. 2007). Although a threat to NZ indigenous ecosystems, in Hawaii it is also a pasture weed (Trujillo 1985). Without biological control, climate change projections suggest that mist flower would become an invasive pasture weed over much of NZ.

An increase of 2 °C is likely to improve the efficacy of BCAs that are limited currently by cool temperatures within the NZ host range, e.g. some glasshouse BCAs may be able to effect control in the field, and *Agasicles hygrophila* Selman & Vogt (Coleoptera: Chrysomelidae) extends its coverage of alligator weed *Alternanthera philoxeroides* (Mart.) Griseb. (Caryophyllales: Amaranthaceae) (Stewart et al. 1995). Conversely, Irish *Microctonus aethiopoides* Loan (Hymenoptera: Braconidae) may perform poorly against the clover root weevil *Sitona lepidus* Gyllenhal (Coleoptera: Curculionidae) in the northern North Island, as currently in subtropical Northland (Gerard et al. 2010).

Non-target impacts

Climate change may alter how BCAs interact with non-target species. With its vulnerable indigenous and productive ecosystems, NZ has legislation and biosecurity processes in place to protect native species and existing biological control systems from non-target impacts (Barratt et al. 2010). The role of temperature was highlighted during risk assessments on a potential fungal BCA for banana passionfruit (*Passiflora tripartita* (Juss.) Poir. and *P. tarminiana* Coppens & Barney Passifloraceae). While host range testing at ambient temperatures in Hawaii indicated adequate host specificity for release in NZ, further testing at NZ temperatures showed that the host range expanded to include the commercial *Passiflora edulis* Sims and possibly the indigenous *P. tetrandra* Banks & Solander (Barton 2005).

The potential for ‘spillover’ damage to non-target species can increase when previously isolated species are brought into contact through spatial or temporal shifts. For example, greater use of lucerne *Medicago sativa* L (Fabaceae) in drought-prone regions would increase the abundance of *M. aethiopoides* in the environment, a species known to attack a range of native weevils (Barratt et al. 1997).

Climate variability

Most biological control systems perform best under a stable environment. Therefore changes in frequency and magnitude of climate extremes may be of more significance than changes in mean conditions. While many species have mechanisms to cope with extremes, they require time to acclimatize and/or enter a resistant state.

Droughts and floods are followed frequently by pest outbreaks because of the loss of BCAs. Field data indicate that parasitoids are generally more sensitive than their hosts, and lag behind in population recovery (Thomson et al. 2010 and references therein). In NZ, outbreaks of a native scarab *Costelytra zealandica* (White) often occur in pasture two to four years after a severe drought (East and Willoughby 1980). Pathogens that limit *C. zealandica* larval populations have limited survival in dry soils (O’Callaghan et al. 1989) and severe droughts that reduce larval populations to low densities result in low infection rates in the next couple of generations.

One distinctive characteristic of NZ’s landscape is its great variety with abrupt contrasts over relatively short distances. This creates many microhabitats that can act as refuges which buffer species against catastrophic weather events and help prevent widespread extinction of BCAs operating in a region. Non-crop habitat manipulation, as in NZ vineyards, also provides shelter (Jonsson et al. 2010).

Host-enemy synchrony

Hance et al. (2007) state that “a key factor determining how climate change may affect the range and abundance of insect populations is the extent to which individual species react independently of the community of which they are a component. Alteration of the synchronisation between host and parasitoids, by divergence of their thermal preferences, can disrupt the equilibrium between host and parasitoid.” This synchronisation need not be perfect: some host escape can stablise an otherwise unstable interaction (Godfray et al. 1994).

Although diapause does not feature strongly in indigenous species, it is retained by exotic species in NZ (Morris 1989). Should the species in a biological control system have contrasting factors regulating diapause, then it is possible for a large mismatch, control failure and local extinction. Above-average warm temperatures in summer 1981 disrupted the diapause-induced synchrony between the horticultural pest, passionvine hopper *Scolypopa australis* Walker (Homoptera: Ricaniidae), and its normally univoltine egg parasitoid *Centrodora scolypopae*

Valentine (Hymenoptera: Aphelinidae) resulting in the parasitoid having an unsuccessful partial second generation (Gerard 2004). Modelling of a simple host-parasitoid system showed that disruption of synchrony once in 25 years did not affect the long-term stability, but the system failed when it occurred more frequently than once in 20 years (Godfray et al. 1994).

Many weed BCAs in NZ are seed feeders and the timing of flowering is a factor affecting BCA performance. Populations of the nodding thistle receptacle weevil (*Rhinocyllus conicus* Frölich) peak in early summer irrespective of region, but nodding thistle (*Carduus nutans* L.) inflorescence densities peak in late summer in the South Island (Kelly and Wood 1991). This poor synchrony results in less than 9 % seed predation compared to 35–50 % in the North Island where the inflorescence densities peak three weeks earlier. Increasing temperatures may improve control in this system in the South Island.

Capacity for evolutionary adaptation

Species have responded to climatic changes throughout their evolutionary history (Root et al. 2003). Where there are no barriers to dispersal, there may be little selection pressure. However, where dispersal is not possible, such as on islands, the rates of evolutionary change in populations under climate change will depend on levels of heritable variation, genetic interactions among traits, and population processes (Lynch and Lande 1993). An important consideration for biological control is that some populations of introduced BCAs possess relatively little genetic variation. For example NZ populations of the herbivorous beetle, *Lochmaea suturalis* Thomson (Coleoptera: Chrysomelidae), introduced for biological control of heather (*Calluna vulgaris* (L.) Hull), are descended from only two females collected in northern England. Genetic studies comparing NZ and UK populations are consistent with severe bottlenecking of the NZ material (Landcare Research unpublished data). It may be possible to reduce impacts of climate change on the efficacy of some NZ BCAs by increasing their genetic variability and potential for adaptation through introduction of additional genetic stock.

Case studies

This section outlines five case studies that demonstrate potential responses of NZ biological control systems to climate change across a range of scales.

Ragwort biological control

This system, using ragwort flea beetle *Longitarsus jacobaeae* (Coleoptera; Chrysomelidae) from Europe to control the northern Eurasian weed ragwort *Jacobaea vulgaris* Gaertn. (Asteraceae), shows how the geographic distribution of BCAs may shift in response to climate change, with resulting changes in local pest suppression. *Longitarsus jacobaeae*, released in NZ in 1983 (Syrett 1989), has proved an effective ragwort BCA (Gourlay et al. 2008). However, ragwort suppression has failed on the west coast of South Island and some higher altitude and/or westerly regions of North Island (Gourlay et al. 2008). The immature stages of *L. jacobaeae* feed on the roots of ragwort, and a study of a closely related species in Tasmania implicates water-logging as a cause of larval mortality (Potter et al. 2007).

Data from three surveys (Gourlay et al. 2005 and references therein) in NZ were combined to produce a relationship of *L. jacobaeae* adult numbers and mean annual rainfall, with an upper rainfall threshold for ragwort suppression around 1670 mm/year^{-1} (Fig. 1). Points above a threshold of 3.5 maximum mean beetles per rosette (the vegetative stage of this biennial) were those sites where ragwort density trends indicated successful biological control while those below 3.5 had no indicationgfs that beetles were reducing ragwort densities. This allowed a preliminary geographic information system analysis (based on an interpolated mean annual rainfall surface, 1971–2000) to be carried out using the thresholds of 1,670 mm/year^{-1} (above which control is likely to be ineffective) and 870 mm/year^{-1} [required for ragwort to survive (Wardle 1987)]. This model produced a map of current successful biocontrol (Fig. 2) which broadly concurs with reports of current *L. jacobaeae* efficacy. The model was then used to estimate how projected changes in rainfall might affect the effectiveness of ragwort biological control in 2040 and 2090 (Table 1).

The climate change projections show an increase from 34.5 % in 2000 to 35.5 % in 2090 in the area where biological control is likely to fail because mean

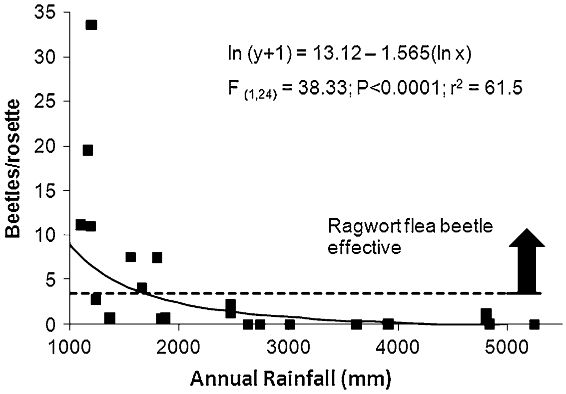

Fig. 1 Relationship between mean *Longitarsus jacobaeae* numbers per *Jacobaea vulgaris* rosette and mean annual rainfall (data from Gourlay et al. 2005 and references therein)

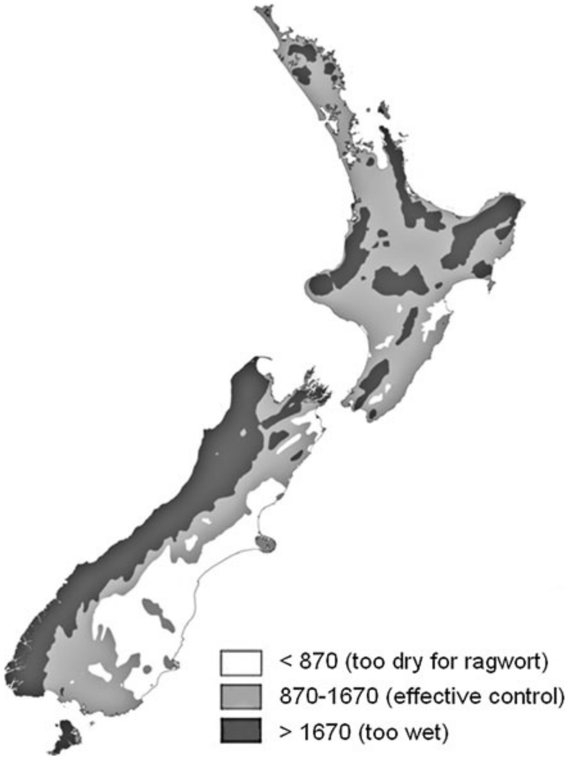

Fig. 2 Mean annual rainfall 1971–2000 showing areas too dry for ragwort (rainfall below 870 mm), where ragwort is usually suppressed by *Longitarsus jacobaeae* (870–1670 mm) and where usually too wet for *L. jacobaeae* (above 1,670 mm)

annual rainfall exceeds the model threshold of 1,670 mm. In the northern part of North Island, where annual rainfall is projected to decrease, areas with effective ragwort suppression should expand (moving from “too wet” to “good control”). In South Island in particular, there should be areas where ragwort extends its range (as rainfall increases above the 870 mm/year^{-1} threshold) but where *L. jacobaeae* should follow the range expansion of the plant and suppress the weed (“too dry” to “good control”). In the east some areas may become too dry for ragwort (“good control” to “too dry”). Overall, although some significant changes are predicted to occur on a local scale, the national level changes to the ragwort-flea beetle biocontrol system as a result of climate change are predicted to be small.

Tomato fruitworm biological control

This case study suggests how climate change may allow more pest generations to develop each season, potentially exacerbating pest threats beyond the ability of current BCAs to maintain effective suppression.

Helicoverpa armigera is the key insect pest of NZ processing tomatoes in the main growing regions in the North Island, where it damages up to 30 % of fruit in unsprayed late season crops (Walker and Cameron 1990). Two larval parasitoids were successfully introduced into NZ to control this pest: *Cotesia kazak* (Telenga) (Hymenoptera: Braconidae) from southern Europe in 1977, and *Microplitis croceipes* (Cresson) (Hymenoptera: Braconidae) from USA in 1986 (Walker and Cameron 1989). These now cause 60–80 % parasitism of *H. armigera* (Cameron et al. 2006). *C. kazak* is the dominant parasitoid and it usually kills before the larvae are able to locate and damage tomato fruit (Cameron et al. 2001). The parasitoids form the basis of an IPM programme to control *H. armigera* on processing tomato crops (Walker et al. 2010).

Helicoverpa armigera normally has three generations per year in the north of the North Island, but in cooler summers and in cooler regions there are usually two generations a year (Walker and Cameron 1990). Despite the parasitoid presence, the third generation can lead to severe crop losses and is an important disincentive to the processing industry from planting late crops of sweet corn and tomatoes.

The timing of *H. armigera* flights in NZ is successfully predicted from a generational day-degree requirement of 475° above a threshold temperature of 11 °C (G. Walker, pers. comm.). These parameters suggest more rapid development in NZ populations

Table 1 Percentage of NZ land area currently in mean annual rainfall classes influencing control of ragwort by the flea beetle *Longitarsus jacobaeae*, and predicted changes in percent NZ land areas in 2040 and 2090

Annual rain 1971–2000 (mm)	% area in 2000	Rainfall change category		Predicted % area in 2040	Predicted % area in 2090
		mm	Explanation		
<870 (too dry for ragwort)	16.7	Always <870	Always too dry for ragwort	16.0	15.4
		<870–>870	Too dry → good control	0.7	1.3
870–1,670 (ragwort usually suppressed by beetle)	48.8	>870–<870	Good control → too dry	0.2	0.3
		Always 870–1,670	Always good control	47.1	46.3
		<1,670–>1,670	Good control → too wet	1.5	2.2
>1,670 (too wet for beetle)	34.5	>1,670–<1,670	Too wet → good control	0.8	1.1
		Always >1,670	Always too wet for control	33.7	33.3

than in Australia (Allsopp et al. 1991) and Japan (Jallow and Matsumura 2001) but slower than those in Greece (Mironidis and Savopoulou-Soultani 2008). Since the threshold temperature for development of the parasitoids is similar to that for the pest (data from Tillman and Powell 1991; Tillman et al. 1993), the generation time ratios (GTR) are constant with temperature. GTR is used as an indicator of biocontrol suppression (Mills 2006). The (GTR) for *C. kazak* GTR = 0.39 is lower than that of *M. croceipes* GTR = 0.52, which matches the observation that *C. kazak* is the more effective BCA (Walker et al. 2010).

These development parameters were used to calculate the expected number of *H. armigera* generations per year across NZ (Fig. 3). The results suggest that even under a moderate emissions scenario, *H. armigera* is expected to become increasingly problematic, and by 2090 may be affecting late season crops of tomato and corn in the eastern South Island plains, where *C. kazak* is not currently present. However, it is not yet known how the parasitoid complex may react under conditions sufficient for four host generations per season, since this does not currently occur in NZ. Given that *C. kazak* has not been as effective at controlling *M. armigera* in warmer areas overseas (Carl 1978), the future viability of the current IPM systems may be compromised in these areas.

Woolly apple aphid biological control

This example shows how differences in the developmental temperature thresholds and diapause behaviours of pest and BCA can interact in different ways, making it difficult to predict the outcomes from climate change.

The woolly apple aphid, *Eriosoma lanigerum* (Hausemann) (Hemiptera: Pemphigidae), is a serious pest of apples throughout the world. It has a short development time, with many overlapping generations per year. In NZ, populations persist year round on the shoots and exposed roots of apple trees, and reproduction is almost exclusively asexual.

Management of *E. lanigerum* in NZ orchards relies on the introduced parasitoid *Aphelinus mali* (Hald.) (Hymenoptera: Aphelinidae) as part of an IPM system (Shaw and Walker 1996). Like its host, *A. mali* has multiple overlapping generations, with 5–15 per year having been reported internationally (Hagen and van den Bosch 1968). However, *A. mali* has a winter diapause as in the Northern Hemisphere (Trimble et al. 1990), whereas the aphid continues to develop year-round. The early spring period is critical in this biological control system, since bud burst creates optimal conditions for reproduction of the aphid before post-diapause parasitoids may have matured. Therefore, the IPM system in NZ may require spring insecticide application to temporarily suppress *E. lanigerum* until *A. mali* becomes active (Shaw and Wallis 2009).

This system contains several factors that suggest that climate change could influence biological control success. First, the aphid and parasitoid differ in their thermal development thresholds: aphid = 5.2 °C (Asante et al. 1991), parasitoid = 8.3 °C (Asante and Danthanarayana 1992). Since the aphid's threshold temperature is lower than that of the parasitoid, a simple GTR model (Fig. 4) shows the GTR is high at

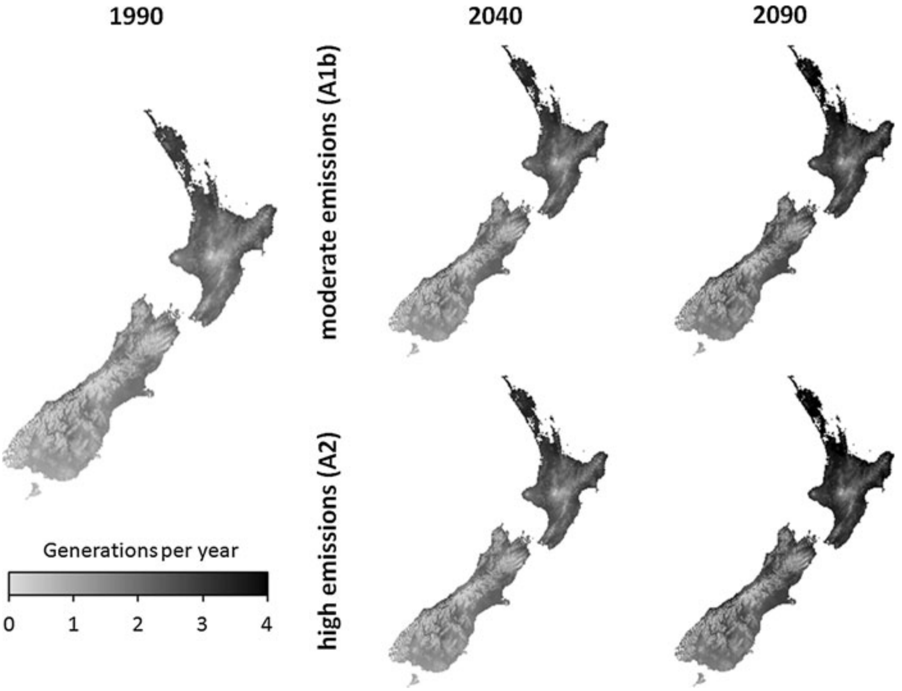

Fig. 3 The number of annual generations of *Helicoverpa armigera* expected in NZ under current and future climates, calculated from a standard day-degree model applied across the 5 km interpolated climate grid

temperatures below about 10 °C, and biological control is expected to be less successful in cool areas. This is indeed the case, with biological control being ineffective in countries with cool, cloudy summers (DeBach and Rosen 1991). Under projected future warming, then, biological control might be expected to be more successful overall. Secondly, if diapause persists under future climates, warmer winters may allow greater aphid population increase during parasitoid diapause and greater damage to orchards in spring. This runs counter to the previous argument which was based on threshold temperatures alone.

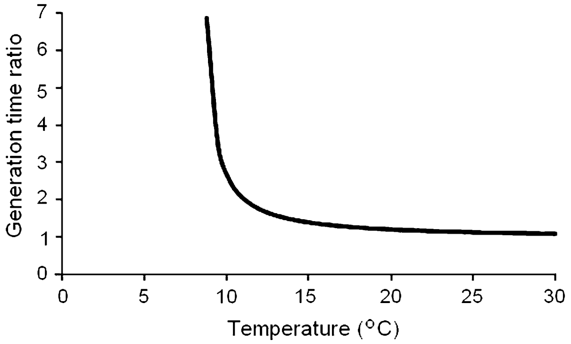

Fig. 4 Generation time ratio GTR for the parasitoid *Aphelinus mali* attacking *Eriosoma lanigerum* at constant temperatures. GTR = 0.95 × (T − 5.2)/(T − 8.3) where T is temperature in °C

Figure 5 shows the predicted GTR for *E. lanigerum* and *A. mali* in NZ under current and future climates, taking both factors into account. This analysis suggests that climate change effects on this biological control system are likely to be minor, with perhaps slightly better suppression overall, especially in the North Island. However, the results suggest that *E. lanigerum* might complete up to one additional generation during the winter, so that pest densities might be slightly greater in early spring. Therefore, a targeted aphicide spray in early spring is likely to remain an important part of the IPM systems for NZ apples (Shaw and Wallis 2009).

Lucerne weevil biological control

This case study exemplifies: (i) how the performance of BCAs can be critically dependent on subtleties of their interactions with host populations, (ii) how a

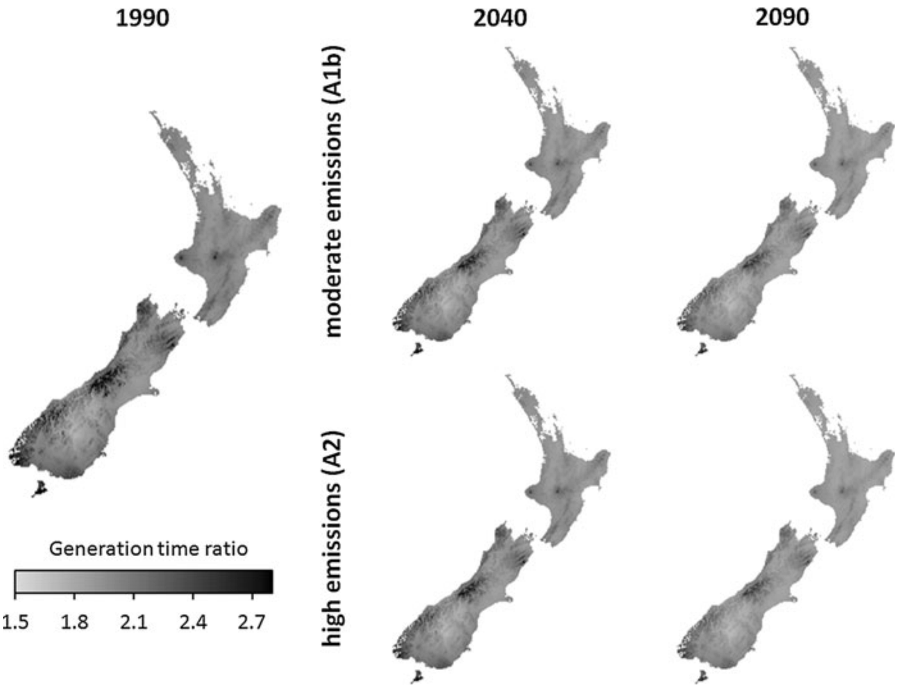

Fig. 5 The influence of future climates on generation time ratio GTR for *Eriosoma lanigerum* and *Aphelinus mali* in NZ, calculated from standard day-degree models applied across the 5 km interpolated climate grid

subtle but critically important population interaction seems to have arisen from a peculiarity of NZ's climate, and (iii) how this could be affected by climate change.

Lucerne is expected to become an increasingly important fodder crop in eastern parts of NZ as they become generally drier. Lucerne weevil, *Sitona discoideus* Gyllenhal (Coleoptera: Curculionidae), a weevil of Mediterranean origin, became a severe lucerne pest in NZ following its discovery in 1975 (Esson 1975). In 1982, a Moroccan biotype of the endoparasitic wasp *M. aethiopoides* Loan was introduced to provide biological control (Goldson et al. 1990).

In NZ, as in Australia (Cullen and Hopkins 1982) and southern Europe (Aeschlimann and Vitou 1988), *S. discoideus* has one generation per year. The weevil aestivates away from the crop and returns in autumn to commence reproduction which continues until spring. The parasitoid over-summers as a non-developing larva in an aestivating host and then resumes its development once its host has returned to the lucerne. Under these conditions, *M. aethiopoides* has two generations for every host generation (GTR = 0.5). This occurs in its natural range in Europe, and in Australia where *M. aethiopoides* is not a particularly effective BCA (Hopkins 1989). However, in NZ, around 3 % of *S. discoideus* populations do not aestivate and remain active within the crop. These weevils support an additional three parasitoid generations. This unusual population interaction reduces the GTR to 0.2, and is thought to be critical to the very effective control of *S. discoideus* exerted by *M. aethiopoides* in NZ (Goldson et al. 1990; Kean and Barlow 2000). The basis for this uniquely NZ population interaction is most likely connected to seasonal differences in climate, interacting with day length, between NZ and other regions such as Australia and Mediterranean Europe.

Projections using the "match climates" functions of CLIMEX (Sutherst et al. 2007) indicate that areas of NZ where the BCA is currently successful may become increasingly similar to Australian areas where it is ineffective (Fig. 6). It is speculated that if the success of *M. aethiopoides* at controlling *S. discoideus* in NZ is related to climate, then as NZ's climate becomes more like that of Australia, there is a risk that this BCA may become less effective (Goldson 2007).

Argentine stem weevil biological control

This case study exemplifies: (i) how within-species genetic variation enables a BCA to adapt to annually changing conditions, and (ii) how this could assist this BCA to cope with climate change.

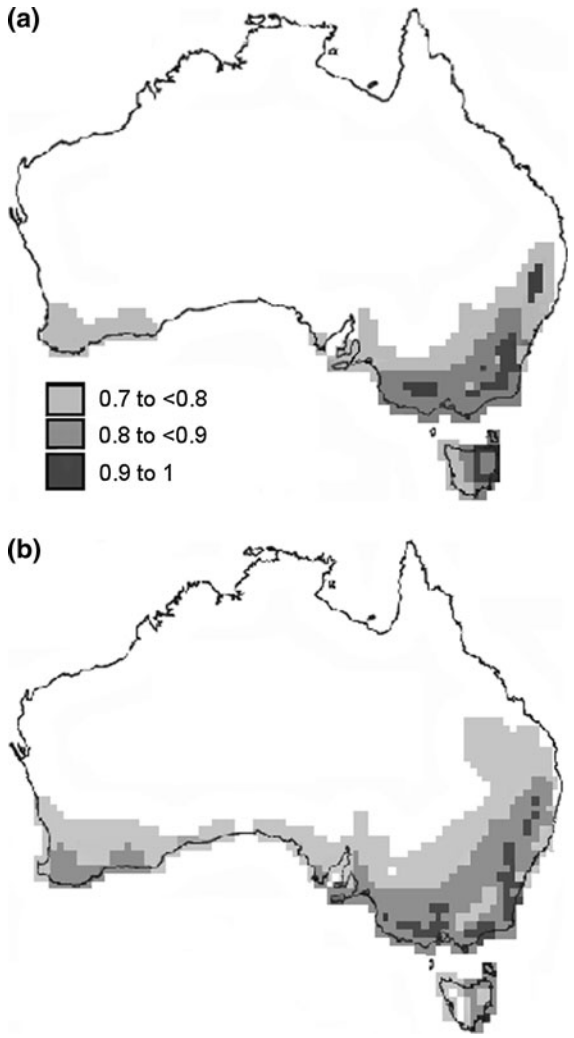

Fig. 6 CLIMEX climate match comparison of **a** 1990 and **b** potential future (2090, scenario A2) climates for central Canterbury (where is *M. aethiopoides* is effective against *Sitona discoideus*) against current Australian climates where *M. aethiopoides* is ineffective

Argentine stem weevil, *Listronotus bonariensis* (Kuschel) (Coleoptera: Curculionidae), was first recorded in NZ in 1927 (Marshall 1937) and now occurs in pasture throughout the country. In 1991, an asexually reproducing South American endoparasitic wasp, *Microctonus hyperodae* Loan (Hymenoptera: Braconidae), was introduced for biological control of *L. bonariensis* (McNeill et al. 2002). Two main *M. hyperodae* genotypes were released, one from east of the South American Andes mountains and another from the west (Phillips et al. 2008).

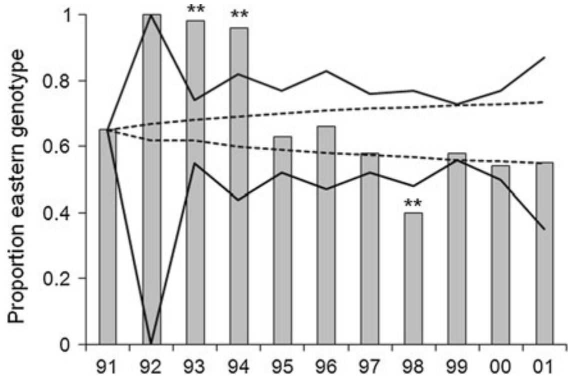

Fig. 7 Frequency of eastern *Microctonus hyperodae* in samples collected at Lincoln, 1991–2001. Dashed horizontal lines show 95 percentile of 10,000 genetic drift simulations and solid horizontal lines show 95 percentile of 10,000 simulations of genetic drift plus sampling error (Phillips et al. 2008). Biotype frequencies that significantly differ from those expected are denoted by $^{**}P < 0.01$

Figure 7 shows the frequency of eastern *M. hyperodae* at the Lincoln site from 1991 to 2001 (Phillips et al. 2008). The eastern genotype dominated in 1993 and 1994, which were particularly cool years, and the western genotype dominated in 1998, which was particularly warm. The presence of both *M. hyperodae* genotypes in NZ has enabled the BCA to make annual adaptive responses to seasonal temperature variations. This has enabled a stronger and more persistent suppressive effect to be exerted on *L. bonariensis* than if just one genotype had been present (Phillips et al. 2008).

At Lincoln, adults of the eastern genotype emerge earlier in summer than western adults (Phillips et al. unpublished). Although few hosts are available for parasitism at this time, it enables an extra parasitoid generation before autumn. In contrast, the western genotype's later emergence coincides with an abundance of hosts, but reduces the number of generations possible before autumn. It is hypothesised that the eastern genotype becomes dominant following seasons with cool autumns because they have an additional generation compared to their western competitors. However, the western genotype becomes dominant when the autumns are warm because it undergoes the same number of generations as its eastern competitor, and had an initial higher reproductive rate (Phillips et al. unpublished).

In Table 2, the above hypothesis was used to show the balance between the *M. hyperodae* genotypes

Table 2 Phenological model projections for the number of annual generations of the weevil parasitoid *Microctonus hyperodae* genotypes from east (E) and west (W) of the Andes under different climate scenarios in NZ

Climate scenario	Cool season (e.g. 1993)		Warm season (e.g. 1998)	
	Generations (E:W)	Dominant	Generations (E:W)	Dominant
Current	2:1	E	2:2	W
2040 A1B	2:2	W	3:3	W
2090 A1B	2:2	W	3:3	W
2040 A2	2:2	W	3:3	W
2090 A2	3:2	E	4:3	E

under projected future climates. Under current climate conditions the dominant genotype will vary between cool and warm seasons, while medium term (2040) warming will generally favour the western genotype, but strong long-term warming (scenario 2090 A2) will favour the eastern genotype. These results demonstrate how climate change is likely to impose new selection pressures on BCAs, and how genetic diversity within BCAs, especially in asexual species, will be important for them to adapt to those new pressures.

Conclusions

The main effect of the projected climate change for the next century in NZ will be for species ranges to move south to follow their preferred climate conditions and shifting crop distributions. However, some species may not, either because of poor dispersal ability or spatially disjoint habitats. A major barrier will be Cook Strait, which may require BCAs to be actively imported into the South Island.

The overall southward trend will be complicated by several factors. First, there is expected to be a change in the frequency of weather patterns resulting in more subtle changes such as the east becoming drier while the west becomes wetter. This will influence the future distributions of some pests and their BCAs. Related to this, the frequency of extreme weather events will increase, which may temporarily disrupt some biological control systems. Pests and their BCAs may respond differently to the north–south influence of temperature, the east–west influence of rainfall, and the unchanging seasonal photoperiod cycle, resulting in unique new combinations for which we cannot currently predict the outcome. In these new situations, the success of biological control systems may depend on adaptation to local conditions, yet many introduced BCAs in NZ may lack the genetic diversity needed for effective adaptation.

Meanwhile, warming in the north of the North Island will open up opportunities for new crops, with their associated pests and diseases. National, inter-island, and local biosecurity are likely to be increasingly important to NZ for managing the associated risks.

In their study of climate change and invertebrate genetic resources for food and agriculture, Cock et al. (2011) observed that there are many gaps in our knowledge of how the beneficial invertebrates in agricultural ecosystems will be affected by climate change. In spite of its dependence on effective biological control systems, this study highlighted that NZ has a similar gaps. There is a need for decision makers in government and industry to understand the wider issues in maintaining effective biological control systems in the face of change and recognition given to the type of information needed.

Acknowledgments The project was funded by MAF Policy (Project 0910-11689) and the paper by the Ministry of Science and Innovation (LINX0804 Ecosystems Bioprotection). The authors thank Barbara Barratt, Jenny Dymock, Linda Faulkner, Travis Glare, Garry Hill, Lynley Hayes Trevor Jackson, Geoff Ridley, Cor Vink, Sue Worner, and Sue Zydenbos for contributing their expert insights, opinions and support at the climate change/biocontrol workshop at Lincoln.

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Author Biographies

P. J. Gerard is a senior scientist with a current research focus on the introduction, release and efficacy of biological control agents for pastoral pests. Other research interests include insect-plant interactions, in particular plant defenses.

J. R. F. Barringer specializes in geographic information system, environmental databases and environmental modelling. His research has focused on digital elevation models, climate variation in the landscape and the relationship of climate, soils and land resources to land-use decision-making.

J. G. Charles leads a team that applies insect biological control to Integrated Pest Management programmes for fruit crops. Current activities include classical biological control of codling moth, woolly apple aphid and various Hemiptera and assessing the threats and risks to New Zealand's native insect fauna posed by exotic natural enemies.

S. V. Fowler has over 20-year experience in weed biocontrol in the UK, USA, New Zealand and various tropical oceanic islands. Currently he leads a research programme that aims to improve the predictability and effectiveness of weed biocontrol, whilst maintaining its excellent safety record and benefit-cost ratios.

J. M. Kean uses population modelling to support decision making for risk analysis and monitoring in biological control and border biosecurity applications.

C. B. Phillips is a senior scientist whose research aims to increase the efficacy of pasture pest management and New Zealand border biosecurity. He is particularly interested both in the determinants of establishment success of accidentally or intentionally species, and in tri-trophic interactions between parasitic wasps, weevils and plants.

A. B. Tait specializes in climate change impacts and adaptation research, spatial interpolation methods of climate data and the application of geographic information system and remote sensing tools for climate analysis. He is a lead author of the Australia and New Zealand chapter of the IPCC Fifth Assessment WG2 Report.

G. P. Walker provides leadership and has 34 years research experience in biological control, development and implementation of IPM programmes for insect pests in outdoor vegetables and field crops.