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FOOD SECURITY

How agro-ecological research helps to address food security issues under new IPM and pesticide reduction policies for global crop production systems

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Abstract

Drivers behind food security and crop protection issues are discussed in relation to food losses caused by pests. Pests globally consume food estimated to feed an additional one billion people. Key drivers include rapid human population increase, climate change, loss of beneficial on-farm biodiversity, reduction in per capita cropped land, water shortages, and EU pesticide withdrawals under policies relating to 91/414 EEC. IPM (Integrated Pest Management) will be compulsory for all EU agriculture by 2014 and is also being widely adopted globally. IPM offers a 'toolbox' of complementary crop- and region-specific crop protection solutions to address these rising pressures. IPM aims for more sustainable solutions by using complementary technologies. The applied research challenge now is to reduce selection pressure on single solution strategies, by creating additive/synergistic interactions between IPM components. IPM is compatible with organic, conventional, and GM cropping systems and is flexible, allowing regional fine-tuning. It reduces pests below economic thresholds utilizing key 'ecological services', particularly biocontrol. A recent global review demonstrates that IPM can reduce pesticide use and increase yields of most of the major crops studied. Landscape scale 'ecological engineering', together with genetic improvement of new crop varieties, will enhance the durability of pest-resistant cultivars (conventional and GM). IPM will also promote compatibility with semiochemicals, biopesticides, precision pest monitoring tools, and rapid diagnostics. These combined strategies are urgently needed and are best achieved via multidisciplinary research, including complex spatio-temporal modelling at farm and landscape scales. Integrative and synergistic use of existing and new IPM technologies will help meet future food production needs more sustainably in developed and developing countries, in an era of reduced pesticide availability. Current IPM research gaps are identified and discussed.

Key words: Ecological services, food security, Integrated Pest Management, landscape ecology, pesticides, ecological engineering.

Introduction

Humans have been farming for about 600 generations, with rapid changes in intensification occurring over the last two to three generations (Pretty, 2009). Food security is rapidly rising up the global agenda due to [1]volatile commodity markets and more frequent and extreme climatic disruptions. These extreme weather events include droughts and floods affecting terrestrial biota in natural and managed ecosystems at multiple trophic levels (Parmesan *et al.*, 2000). We live in an era of unprecedented human population growth, whilst concurrently facing global threats (Tilman et al., 2001) from climate change, economic uncertainties, rising energy costs, and tougher crop protection regulations (e.g. 41/4114/EEC and 2009/128/EC). The United Nations predicts that there will be more than 4 billion people living under water scarcity by 2050, up from 0.5 billion in 1995. In addition, global per capita cropland is less than half of the 1961 availability. More than 900 million people are now classified as hungry or malnourished. Global food production is claimed to be adequate by the FAO. They blame food insecurity on lack of available land for poorer farmers, inadequate food distribution, unemployment or low incomes (worsened by the severe global economic crisis), and the excessive costs of domestic staples as the main factors driving hunger in developing countries (FAO, 2002, 2009). The global population is set to increase to around 9.1 billion by 2050 (Engleman, 2009), with the per capita consumption increasing in several developing countries, including China and India. The fact that hunger was increasing even before the current food and economic crisis suggests that present solutions to food production and malnutrition are insufficient.

Intensive agriculture in developed countries raises a further set of issues. For example, recent EU reviews of pesticides have led to policies which have caused the

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withdrawal of over 60% of active substances from the European market, with both major and minor crops being affected. The changes to 91/414/EEC in 2010, based on hazard estimates rather than risk assessment of human health and environmental impacts, will further reduce pesticides available to the UK and other EU member states. In addition, tightened Maximum Residue Limits (MRL) legislation and new Sustainable Use of Pesticides and Water Framework Directives will further limit the use of the remaining pesticides, particularly herbicides. These trends present a huge challenge to many sustainability issues, not least to food production, particularly when weeds, pests, and diseases cause major crop losses despite costly agricultural inputs (pesticides, fertilizers, fossil-derived energy). A recent survey (Eurostat, 2007) demonstrated that, despite having only 8% of the world's agricultural area, the EU is the world's largest producer, user, and exporter of pesticides. In 2007, the global crop pesticides market was $33.19 billion, of which EU member states alone accounted for $10.42 billion (31% of the global pesticide market).

Despite costly and increasing inputs of pesticides (insecticides, fungicides, herbicides), current figures for global crop losses still show that pests, diseases, and weeds are reducing food availability and security considerably. For example, global crop losses due to pests are reported in the order of 26–29% for soybean, wheat, and cotton, while losses for maize, rice, and potatoes are in the order of 31%, 37%, and 40%, respectively. In cotton under severe pest attack, losses can be as high as 80% (Oerke, 2006). Despite a clear increase in pesticide use over the last 40 years (a 7-fold increase in pesticide tonnage used; Tilman et al., 2001), crop losses due to pests have not decreased significantly during the same period. At the same time, global human populations have increased by approximately 2.6-fold. To put crop losses due to insect pests into a human perspective, it is estimated that the amount of food that insects consume (pre- and post-harvest) is sufficient to feed more than 1 billion people. By 2050 it is thought that there will be an extra 3 billion people to feed. During this timescale it is likely that insects will increase in numbers and in pest types. These pests are likely to have less predictable behaviours and migratory range, due to more variable climate change factors. These predicted pest increases are supported by insect fossil records during historical periods of rapid climate change and by recent trends (Currano, 2009; Gregory *et al.*, 2009; Lu *et al.*, 2010).

Can IPM research help in another 'green revolution', using 'ecological engineering' approaches?

Several options are discussed in terms of increasing food production and agricultural sustainability using 'ecological services' (ES). Most ES combinations involve 'trade-offs' (Pilgrim *et al.*, 2010): for example, we could expand cultivation into new lands, but then risk further loss of biodiversity and associated ES, valued at around $33 trillion/year (Costanza *et al.*, 1997). Of this figure, beneficial insects provide key pollination services to crops and biocontrol of pest species, with these ES valued by Costanza's study at $\$117\times10^9$ and $\$417\times10^9$ per year, respectively. The challenge, therefore, is to reduce crop losses due to pest species whilst still conserving key beneficial species providing ES. Therefore, species-selective measures are needed, tailored to specific agro-ecosystems, within a policy-driven framework of reducing pesticide usage and adverse impacts.

Biological control has been practised for many centuries, particularly in poorer and warmer countries which have serious pest problems but which generally cannot afford expensive pesticide inputs. Modern research on the development and integration of several combined pest control measures (IPM) can be traced back to 1959 at the University of California. A seminal paper was published by Stern *et al.* (1959) on the integration of chemical and biological control of the spotted alfalfa aphid. In this study, they defined now widely used IPM terms including 'economic thresholds', 'economic injury levels', and 'general equilibrium levels'. These ideas later evolved to include concepts of IPM blending and harmonizing several multifaceted approaches. These included breeding for durable pest resistance and the use of semiochemicals (particularly insect attractants and repellents) and combined ecological strategies like 'push–pull' and companion cropping to manage pests, diseases, and weeds (Khan *et al.*, 2010; Pickett *et al.*, 2010).

The current aim is to combine these 'IPM tools' in an organized way and to optimize them in 'IPM toolbox' packages for specific agro-ecosystems. For this, a detailed understanding is needed of 'systems level' ecology, focused on agricultural food webs. This agro-ecosystem approach involves knowledge of soil organisms, crop and non-crop plants, multiple herbivores, several guilds of natural enemies (e.g. predators and parasitoids) and sometimes superparasites at higher trophic levels. It is predicted from co-evolutionary theory (Fagan *et al.*, 2009) that additive or synergistic interactions between IPM tools can increase the durability of individual IPM components (e.g. recent technologies including pest-resistance genes and more targeted pesticides) and thus make the whole IPM package more sustainable, both environmentally and economically. The main scientific challenge is to learn how best to apply fundamental ecological knowledge to crop protection at the field, farm, and landscape scales.

Scientists are currently designing and testing farmer-friendly 'IPM packages' which work together at the farm scale to reduce pesticide inputs (particularly those targeted under policy 91/414 EEC). A closely related aim is to reduce selection pressure on any one part of the system. For example, the risk of development of pest populations with resistance to pesticides or with the ability of pests to overcome host plant resistance genes in crops could be reduced considerably by using multiple tactics within a well-designed IPM programme.

Does IPM really work at the farm level in varying climatic conditions and in broader crop production? In a recent survey of 62 international IPM projects covering 26 countries and 25.5 million ha of crops including rice, maize, wheat, sorghum, vegetables, potato, cotton, and legumes, over 60% of the projects resulted in reduced pesticide inputs and increased yield. On average, yields increased by 40% and pesticides were reduced by 60% (Pretty, 2005), indicating a broad potential for IPM globally.

IPM research: understanding underpinning agro-ecology using case studies to inform on system interactions

Plant breeding for pest and disease resistance in IPM

The use of pest-resistant crop cultivars is a key foundation of a durable IPM programme. At JHI, together with MRS Ltd and other plant breeding groups, soft fruit, cereals, and potatoes have been developed with genetic resistance to key pests and pathogens including raspberry aphids, potato blight, and barley yellow mosaic virus. New biotechnologies including marker-assisted selection (MAS) methods, Quantitative Trait Loci (QTL) analysis of complex genetic traits, and improved plant transformation methods are helping to speed up the process of getting new pest-resistant crops on to the global market. For many crops this typically still takes more than 10 years, so long-term planning and funding security is required.

Co-evolutionary battles between pests and plant resistance genes: a UK soft fruit case study

The reliance just on pest- or disease-resistant crops, with typically one or few major resistance genes in their genetic background, inevitably produces strong selection pressure and crop protection failure. Pests including many aphids, which have both sexual and asexual reproductive strategies in a single growing season, provide a formidable challenge to the use of pest-resistant cultivars, because they can rapidly evolve counter-adapting virulent biotypes against single crop protection strategies. This is well demonstrated by long-term research and plant breeding for raspberry aphid resistance in the UK at JHI and East Malling Research and in the USA (Birch *et al.*, 1994; Daubeny, 1980; Sargent *et al.*, 2007; Birch and Begg, 2010). Virulent biotypes of the large raspberry aphid, *Amphorophora idaei* (Börner), overcame the first aphid resistance gene in about 40 years of commercial use, but have overcome a replacement aphid resistance (R) gene in less than 10 years of cultivation (Fig. 1). There is a strategic 'tipping point' for such pests, where they can now overcome single control measures (e.g. R genes or pesticides) in a shorter time than scientists can develop new pest control solutions for crops including lettuce, melon, sorghum, and wheat (Dogimont *et al.*, 2010). This co-evolutionary process speeds up considerably in environments where temperature, humidity, carbon dioxide, and shelter all favour pests with rapid, asexual reproductive strategies (e.g. aphids attacking crops in protected cultivation under glass or plastic). For example, growing high-value crops like raspberry under plastic tunnels has increased the window of pest attack from 2–3 months (open field plantations) up to 10–11 months (polytunnel cultivation) for the main virus vector aphid, *Amphorophora idaei.* This change in crop management within polytunnels has also provided a more suitable micro-climate for two additional aphid pest species, *Aphis idaei* van der Goot (small raspberry aphid) and *Macrosiphon euphorbiae* Thomas (potato aphid) to thrive over an extended cropping season. Prior to protected cropping, these two aphid pest species were minor pests of raspberry, but have surged with changing crop management including extended growing seasons and 'green bridges'. Compared with aphid infestations in open field plantations of the same crop varieties, there are now twice as many large and small raspberry aphids (important virus vectors) and 25 times more potato aphids (potential virus vector) attacking protected raspberry crops in polytunnels (Birch and Begg, 2010) than under the previous crop management system. This indicates that changing climate and crop management are interacting to make some pest problems dramatically more serious than 10 years ago. This increasing pest threat is occurring just when key pesticides are being withdrawn under EU (91/414/EEC, 2009/128/EC and related Directives) and global crop protection regulations and when pest-resistance genes are breaking down under the intense selection pressure caused by extended cropping and climate change. On the positive side, under protected cultivation (e.g. in plastic tunnels and in greenhouses) certain key predators including spiders and hoverflies are greatly enhanced (a 2–6-fold increase for different natural enemy groups found on raspberry) compared with the open field plantations. This opens up new research and commercial opportunities for biocontrol as an IPM tool for soft fruit and other high-value protected crops where the cost:benefit ratio readily supports investment in IPM programmes (Birch, 2008; Birch and Begg, 2010). These studies also demonstrate how small changes in climatic conditions which are accumulated over an extended growing season can have a large effect on the complex interactions in

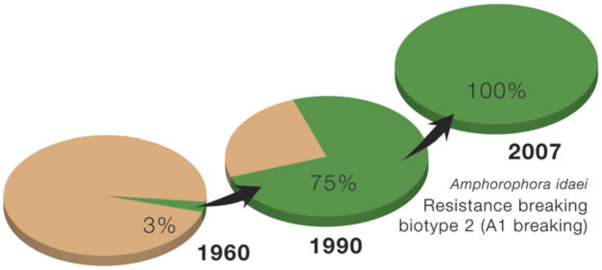

Fig. 1. Effect of selection pressure on virulent raspberry aphid biotypes (green sector) when a single control measure (a single, major gene resistance) is used in a raspberry monoculture system (Birch *et al.*, 1994, 2004).

agricultural food webs and lead to new pest and disease problems.

Use of semiochemicals in IPM: an EU soft fruit case study

UK and EU collaborative research groups have developed novel, multi-disciplinary approaches involving entomologists, phytochemists, and biophysicists to identify novel pest attractants and repellents. For example, scientists are using fundamental chemical ecology knowledge to develop and commercialize the first precision monitoring trap for raspberry beetle, in collaboration with grower consortia, specialist crop protection and IPM companies, and major supermarket chains. Multi-disciplinary studies of flower volatile chemistry (Robertson *et al.*, 1994), chemical ecology, insect behaviour, and insect antennal electrophysiology provide a way of using 'biomimicry' to fool the specialist pest into a trap that represents a giant host flower in terms of key host recognition signals (colour and smell) for this pest. This trap is now being successfully used for precision monitoring on farms in the UK, Norway, Sweden, and France to reduce the application of selective insecticides to pest 'hot spots' in plantations, based on weekly catch thresholds (Birch *et al.*, 2004). In concurrent on-farm trials this IPM approach, using raspberry beetle traps as monitoring tools, gave similar levels of crop protection as the farmers' standard practice, using currently recommended synthetic insecticides (Birch and Begg, 2010). The same type of precision monitoring approach is now being developed for other types of pests in the UK and across the EU and Scandinavia under a new wave of IPM-related funding to address the EU 'pesticide gap'. Herbivore-induced plant volatiles (HIPVs) are also now being tested to manipulate the behaviour of both pests and their natural enemies (Orre *et al.*, 2009), although it may be difficult to use these without disrupting complex trophic interactions important in conservation biocontrol which rely on finely balanced volatile signals (Jonsson *et al.*, 2008).

Optimizing agricultural food webs for biocontrol in IPM: annual and perennial crop case studies in the UK

Long-term studies on agro-ecosystems and their rotations are now considered a priority, focusing on both perennial and annual systems. Hawes *et al.* (2009) used data from the GM crop Farm Scale Evaluations in the UK to demonstrate that, in the arable (annual) systems studied, there was strong evidence of 'top down' control on herbivores by generalist predators and more specialist parasitoids. They also found strong evidence of a 'bottom up' effect of weeds and crops as hosts for herbivorous invertebrates. This combined 'top down' and 'bottom up' regulatory effect on pest insect populations is also found in results obtained from ongoing experiments comparing food webs in perennial agro-ecosystems using field-grown versus protected raspberries in polytunnels (Birch and Begg, 2010). Raspberries provide a unique UK example of a crop plant conventionally bred to contain several types of genetic resistance to pest aphids and provide a good research system for studying the effects of selection pressure on R gene durability. In long-term on-station and on-farm studies, several aphid resistance genes provide a strong 'bottom up' effect on aphid populations, complemented by 'top down' effects of several key natural enemies (biocontrol agents) including spiders, hoverflies, and entomopathogenic fungi. These biocontrol agents can operate in a 'top down' manner much more effectively in the protected crop (polytunnels) than in the open field, thus helping to offset the large increase in three different aphid species under this warmer, season-long microclimate. Thus additive interactions on agricultural food webs can be seen between longer term climate change trends (e.g. milder winters) and more rapidly changing crop management practices (e.g. green bridges for pests and diseases in protected crops). These factors now combine to create increased pest pressures in the UK and the EU, comparable with pest pressures in more southerly or tropical regions with milder and more humid climates.

Compatibility of IPM with biotechnology: biosafety issues

The potential contribution of GM cropping to IPM has been examined mainly for herbicide tolerance and insect resistance, but the issues debated have implications for IPM in general and could be extended to any major change or introduction of new technologies to cropping practice. Among the main issues are the choice of comparator in any experiment or assessment and then the quantification of that comparator, especially in terms of its background variation over time and the 'ecological context' of new technologies within the upper and lower limits of effect caused by existing agronomic and climatic factors (Squire *et al.*, 2005; Birch *et al.*, 2007). Examples to date have mostly used a small set of indicators, a comparator that is generally analogous to that used in assessments of food safety, i.e. familiar, with a history of safe usage (EFSA, 2006) and timescales of one to a few years. However, there are potentially serious problems with this approach to the assessment of the risk of GM cropping and hence its suitability as a component of IPM (Squire *et al.*, 2005; Birch *et al.*, 2007).

Taking the example of the UK's GM crop trials, still the most highly replicated in the world, the primary question was whether weed management using herbicide-tolerant GM crops had different effects on the biodiversity of fields than current conventional practice (Firbank *et al.*, 2003; Squire *et al.*, 2003). Because of immediate concerns for farmland biodiversity, the experiment was tightly focused on in-field plants and invertebrates and did not cover other potential impacts, for example, on element cycles or pesticide losses from the fields. Neither did it consider the yield of the crops and hence it was unable to examine trade-offs between the economic and environmental consequences of the technology. Admittedly, considerable extra cost would have been incurred in these trials if these extra indicators had been measured. The comparator was conventional weed management as practised in commercial agriculture (Champion *et al.*, 2003), but while this comparator might be 'familiar' to farming, its history of safe usage is arguable. For the crops of beet and oilseed rape in the study, the outcomes of the ERA (Environmental Risk Assessment), supported by other work in Europe, were that arable biodiversity was in danger of being further depleted if GM herbicide-tolerant crops were commercialized (Heard *et al.*, 2003).

On the other hand, the emerging conclusions for insect-resistant *Bt* maize in Europe (Birch *et al.*, 2007; Cortet *et al.*, 2007; Griffiths *et al.*, 2007) are more favourable to this GM trait type and included little or no long-term negative impact on biodiversity, reduced pesticide usage in most regions (partially dependent on pest pressure), and limited spread and transfer of impurity to other crops (Messean *et al.*, 2009).

More generally, the arguments for a comprehensive approach to ERA are more compelling. First, the range of ecological processes and indicators should be broader and the assessments should not be confined only to negative effects. As for any other technology, there may be ways to mitigate a negative if positives are demonstrable and have significant benefits over current practices (May *et al.*, 2005). Broadening ERAs should consider an economic appraisal (cost:benefit) and the inclusion of indicators for biogeochemical cycles and potentially diffuse pollutants affecting landscapes (Tank *et al.*, 2010). Any indirect effect on them—for example, if the amount of nitrogen fertilizer were increased, or pesticide usage changed due to secondary pest outbreaks (Lu *et al.*, 2010)—would probably far outweigh, in terms of whole-system impacts such as carbon footprint (Hillier et al., 2009), any direct effect of a GM crop on biodiversity. Inversely, the mitigation of any negative effects would be worth pursuing if any reduction in the use or wastage of pesticides, N or P were found.

Second, the comparator may have to be different from the familiar product with a history of safe usage. Since many aspects of current cropping practice have negative effects on ecological processes, such as the ability of the soil to carry out essential functions, typical current practice may not be the most appropriate for environmental risk assessment. Therefore, comparators might include a range of practices, or even a possible optimal or target ecological state that should be aimed for. This argument may be extended to a 'system-first approach' as proposed by the SIGMEA project on GM coexistence and ecological risk carried out by many partners in Europe (Messean *et al.*, 2009). Here, the range of conditions under which the system might vary without long-term harm should be determined by reference to a broad set of indicators. The question would be 'what crop types and cropping practice does the system need to get it to such a state and keep it there' rather than 'what is the effect of this or that innovation' (Squire *et al.*, 2010). The SIGMEA project concluded; 'standards and criteria for environmentally resilient cropping systems are needed against which GM cropping and its non-GM comparator can be assessed. Setting such environmental standards is now an absolute priority.' Moreover, trade-offs in key 'ecological services' (ES) need to be carefully monitored so that gains in one ES are not lost by the reduction of another ES (Pilgrim *et al.*, 2010).

Third, the scales of time and space over which the assessments are made needs careful consideration (BEETLE report, 2009). Responses by indicators to a GM plant may be different, even in direction, between laboratory, greenhouse, and field (Birch, 2008). Effects on biodiversity may differ from averages among fields to cumulative values in the landscape (Squire *et al.*, 2009). No amount of testing in laboratory-controlled conditions can mimic the complexity of the field and the changing environment over multiple seasons.

A pragmatic way forward may be to assess the existing range, variation and trends in indicators as a context into which the new technology is introduced, for example, an existing IPM programme. The question can then be asked, how great an effect would the innovation have to have on the system for it to be noticed above the background 'noise'? An example of a move towards this approach is an assessment of the paired time series of percentage crop and weed cover in the UK's GM crop trials referred to earlier. The time series of crop cover in oilseed rape grouped into different profiles, or shapes, that were largely independent of the season of sowing or the weed management. The weed cover was more strongly influenced by the crop cover time series than the GM treatments. Here, the main determinants of weed cover (and therefore weed biodiversity) were the, albeit unidentified, factors of the site and weather; the signal of the GM treatment was detectable but small and specific compared to the noise (Debeljak *et al.*, 2011).

Dealing with heterogeneity in IPM

Heterogeneity is a fundamental property of ecological systems and remains so in an agricultural setting. The spatial and temporal pattern of cultural practices and pesticide treatments of crops adds heterogeneity to the habitat mosaic experienced by pest organisms (weeds, insects, and microbial pathogens) as does variation in the suitability and resistance of hosts. The movement or dispersal of pests across this mosaic is the rule rather than the exception, so that understanding and working with this heterogeneity is essential for the regulation of pest populations and a growing part of IPM research.

Defining the functional biological unit

Identifying the scale or scales at which heterogeneity is most influential is an important aspect of this work (Birch *et al.*, 2007). A reasonable starting place to achieve this is the characterization of the spatial distribution of pest populations, the patchiness of which often follows from processes relevant to their regulation and control (Rahman *et al.*, 2011). Defining the correct scale relies not least on the identification of the most appropriate functionally distinct unit. Species will continue to provide a useful first approximation, but recent work has shown that several species may be functionally equivalent (Hawes *et al.*, 2009) while intra-specific biotypes exist for a wide range of pest species. The management of pest biotypes is an essential goal of IPM strategies where pest biotypes have differential resistance to (ability to overcome) current control strategies (Birch *et al.*, 1994). However, the importance of intra-specific pest variants (biotypes) is unlikely to be limited to cases of differential resistance but will extend to those of more general ecological significance. As an example, weed species can possess considerable intra-specific functional variation (Hawes *et al.*, 2005) including differences in life-history strategy (Iannetta et al., 2007; Toorop *et al.*, 2008), and interactions with insects and pathogens (Iannetta *et al.*, 2010; Karley et al., 2008) that are associated with spatially segregating, genotypically distinct populations. Recognizing such ecotypic variation and the population structure that underlies it is essential for the effective and targeted deployment of IPM strategies.

Reinstating diversity in the crop

The 'controlled environment' nature of intensive agriculture sees the widespread deployment of a few crop species and varieties (typically as monocultures) designed for optimal performance under a narrow range of conditions, together with the loss of non-cropped habitats such as woodlands, wetlands, and hedgerows, so that there has been a reduction in diversity and habitat complexity (Benton *et al.*, 2003). The refinement and simplification of intensive agricultural systems has led to instability that requires constant intervention to maintain productivity. It has been anticipated that reintroducing habitat diversity and complexity will return agro-ecosystems to a position of ecological balance and reverse the adverse effects of intensive agriculture (Nicholls and Altieri, 2004).

Increasing crop diversity at the field scale, through the use of varietal and species mixtures, can suppress pests while also increasing yield, quality, productivity, and stability (Newton *et al.*, 2009; Vandermeer, 1989). Careful design of crop variety mixtures accounting for G×E effects is important to ensure combinations of traits that provide the complementarity and facilitation underlying these benefits (Newton *et al.*, 2009). The effectiveness of variety mixtures is also sensitive to the scale at which components are deployed (i.e. the area below which crop genotypes are not mixed), although the nature of this response appears variable with many studies, showing a benefit from deployment at smaller scales but others being more effective when deployed at larger scales (Newton *et al.*, 2009). These conflicting results may be accommodated by a common hypothesis if, in conjunction with the loss of apparent diversity at large deployment scales, it can be shown that a scale exists below which the additional diversity is no longer behaviourally or functionally resolved by the pest organisms. This leads to an optimum scale of deployment defined by the life-cycle and dispersal characteristics of the pest.

Engineering large-scale heterogeneity

Heterogeneity can be introduced into the arable system at a larger spatial and temporal scale by the addition of semi-permanent, non-cropped habitat features. Such 'ecological engineering' to enhance habitat heterogeneity is the primary mechanism of conservation biocontrol (Landis *et al.*, 2000). The inclusion of features such as wildflower borders, grassy buffer strips, and hedgerows are all examples of conservation biocontrol (Jonsson *et al.,* 2008) that have beneficial effects through the provision of disturbance refuges, overwintering sites, and food resources. The potential to suppress insect pests by promoting natural enemy assemblages in this way has been extensively tested and shown to be successful. However, the complexity of the interactions between pest and natural enemy assemblages including, for example, niche complementarity, intraguild predation, and functional redundancy means that these mechanisms can also fail to enhance natural enemies in a way that achieves optimal levels of predation or pest suppression (Straub *et al.*, 2008). Moreover, the best way to manipulate the habitat needs to be viewed in a spatial context and at a landscape scale (Tscharntke *et al.*, 2007) as the population dynamics of pest and natural enemies typically range across scales well beyond that of the habitat feature itself. The available evidence supports the contention arising from this, that landscapes influence pest assemblages, showing that weeds (Roschewitz *et al.*, 2005), microbial pathogens (Plantegenest *et al.*, 2007), as well as arthropods (natural enemy and pest species; Tscharntke *et al.*, 2008) respond to broad landscape characteristics such as fragmentation and complexity.

Therefore, pest-suppressive landscapes could be designed as a part of area-wide IPM (Koul *et al.*, 2008) and also the recently proposed 'pattern–process–design' paradigm of landscape ecology (Nassauer and Opdam, 2008). For conservation biocontrol this represents a development of existing 'ecological engineering' strategies as exemplified by the role of 'spill-over' biocontrol effects, the use of 'green corridor' features to link fragmented landscapes, and the role of meta-population dynamics (Tscharntke *et al.*, 2007). Despite a growing simplification in many parts of the world, farming landscapes of Europe have retained a degree of complexity. Where crop rotation has largely been retained, European arable landscapes remain dynamic entities of changing composition and configuration. This provides scope to manage crop diversity at the landscape scale with the objective of contributing to pest suppressive landscapes. The effectiveness of such an approach depends essentially on the heterogeneity experienced by pests across the crop types. Crop type is a major determinant of the composition of weeds communities (Fried and Norton, 2008) and arthropod and microbial pests where a degree of host specificity is common, and scope to manipulate this further exists through spatial deployment of pesticides and pest-resistant genotypes, the potential of which has recently been demonstrated (Hutchison *et al.*, 2010). Experimental approaches are difficult to implement at the landscape scale and so modelling approaches take on particular importance in unravelling the spatial and temporal dynamics of pest systems (Jongejans *et al.*, 2008; Ostfeld *et al.*, 2005). For example, using a meta-community model it has been possible to demonstrate potential mechanisms by which crop heterogeneity can regulate weed abundance while still promoting diversity and that cropping patterns can, in principle, be managed to harness this effect (Begg *et al.*, 2010).

The heterogeneity of arable systems affects populations and habitats across multiple scales and adds considerable complexity to the functioning of interacting pest–plant systems and pest regulation. Acknowledging that the ecology of a pest is not restricted to an individual field but is played out across a broad landscape requires this heterogeneity to be accommodated in the design of a single pest-suppressive landscape. However, the challenge does not stop there, sustainable agricultural systems demand landscapes that accommodate trade-offs between all relevant ecosystem services and not just pest regulation (Rodríguez *et al.*, 2006).

Table 1. Predicted research needs to optimize IPM components

IPM technology	Potentially negative factors	Potentially positive factors	Research gaps for successful IPM
Synthetic pesticides	Broad spectrum products can adversely affect non-target organisms in biocontrol. Over-use can lead to pesticide resistance and secondary pest upsurges. Residue issues on food (especially fresh produce). Potential exposure issues for farmers and consumers.	Narrow spectrum products give fast and effective control and are mainly compatible with biocontrol. Good network of crop protection advisers. Good farmer knowledge, especially in developed countries. Targeted pesticide spraying using monitoring and thresholds reduces residue risks.	Optimize products and application methods for new pest-resistant crops (GM and conventional). Analyse 'pesticide' gaps caused by new policies and prioritise those pest/crop combinations most affected in the short–medium term. Optimize with biopesticides to minimize non-target impacts. Early detection and management of pest and disease 'hot spots' to reduce whole crop pesticide inputs.
Biopesticides	Some are slow acting and need specific environments to work well. Possible non-target effects on biocontrol.	May be less harmful to agro-ecosystems. Possibly less food residue issues (but case specific).	Develop reduced dose combinations of pesticides and biopesticides compatible with biocontrol against pest complexes.
Pheromones and plant-derived semiochemicals	Blend and release rates must be precisely controlled. Expensive on a large scale. Registration currently too costly for niche markets (but changing in EU).	Species-specific control. Also useful for precision monitoring	Develop combinations of sex pheromones and host plant volatiles to increase efficacy. Develop cheaper and more effective release systems for area-wide IPM. Use of synthetic herbivore-induced volatiles to enhance biocontrol.
Biocontrol	Sometimes too late or too slow to suppress pests with high reproductive rates (e.g. aphids). Work best in protected cultivation.	Can complement the use of pest-resistant cultivars, which also facilitate reduced pesticide use (e.g. *Bt* expressing GM cotton).	Need to develop biocontrol and breed for pest-resistant crops in parallel, to be more cost- and time-effective. Augmentative and early release of biocontrol agents. Use of floral rewards (e.g. specific wild flower mix strips) to enhance biocontrol within the crop.
Pest-resistant cultivars	Can select for virulent pest biotypes, reducing sustainability. Normally only controls one target pest type. Long-term strategy (10+ years).	Complements biocontrol. Helps to reduce pesticide inputs.	Need to speed up plant breeding, testing and biosafety using biotechnology. Need to combine multiple types of resistance traits without causing yield penalties.
'Ecological engineering' of fields and landscapes	Loss of cropped land. Spatio-temporal complexity. Scaling-up issues (fields to farms to regions). Long-term strategy, requiring regional co-ordination and co-operation.	Complements biocontrol and area- wide IPM. Makes use of on farm and regional biodiversity to deliver ecological services (e.g. biocontrol). Regional benefits to co-operating farmers.	Needs development and validation of spatio-temporal models (scenario testing at regional scales). Improve efficacy of biocontrol using new techniques including 'attract and reward' and region specific wild flower rewards for natural enemies. Multi-disciplinary teams required to provide data requirements (e.g. entomologists, pathologists, weed ecologists, GIS experts, modellers, climate change experts, agronomists).
Farmer and consumer awareness	Understanding complex social, economic and environmental interactions. Acceptance of 'external costs' of farming to societies. Confusing labelling and traceability of food grown using IPM or other more sustainable systems.	Social learning and grower education programmes, including public demonstration events on-farm. Using appropriate resource economics techniques, growers' variable costs for energy, pesticides and labour can be reduced using IPM.	Ways to engage farmers at the start of IPM research programmes, when defining problems and solutions. Demonstration of significantly reduced pest damage from IPM under different conditions, alongside increased crop yields, quality and grower profits. User-friendly communication of long-term eco-service values to consumers and policy-makers.

Research priorities for optimizing IPM: multi-disciplinary teams and applied outcomes

For IPM to succeed in the UK, EU, and globally for major and minor crops, as it has done in many other countries globally (Landis *et al.*, 2000; Pretty, 2005), a holistic, systems-based approach is needed that makes use of potential synergies between entomologists, pathologists, chemical ecologists, plant ecologists, phytochemists, plant geneticists, plant breeders, biotechnologists, agronomists, and mathematical modellers. This is a medium to long-term approach (Heinrichs *et al.*, 2009), particularly when based on a foundation of durable pest and disease resistance in new crop cultivars. As explained previously, several crop protection strategies are now at a strategic 'tipping point' where pest biotypes are winning the co-evolutionary battles against current protection measures, exemplified by pests with greater ability to overcome both pesticides and R genes. To protect the long-term investment in plant breeding, biopesticide development, and IPM these strategies need to be integrated at the research level, then driven through to applied outcomes with commercial partners. This will also require a shift in research effort from fundamental to applied aspects, with concomitant career rewards for scientists who move away from research driven by questions outside the ecological context and from publishing in high impact fundamental science journals. For optimal effectiveness and progress, fundamental and applied researchers need to work closely together across multiple disciplines, then design IPM products and strategies that are simple and affordable enough for farmers. On-farm research with participating growers is the most convincing way to demonstrate that IPM really works at a local or regional level.

Can IPM researchers respond in the short term too, to address pesticide gaps? Strategic assessment (pesticide 'gap analysis') of key pest/crop combinations most likely to be at highest risk under EU pesticide reduction legislation is urgently needed. The research focus (see Table 1) should now be on components of the expanded IPM toolbox that can be delivered to the farming industry within the next five years. These IPM tools will include precision monitoring tools for pest and diseases (now referred to as 'IPDM', when disease control is integrated), targeted spray technologies, and enhanced biocontrol of key pests using the augmentation of endemic natural enemies and forecasting tools based on multi-trophic models. In addition, understanding the spatial and temporal factors affecting food webs in agro-ecosystems (e.g. the EU PURE IPM project, involving SCRI and several other centres of expertise in the EU) will greatly help to develop more sustainable crop protection strategies using the latest technologies for introgression of combined pest and resistance traits (Birch and Wheatley, 2005; Birch and Begg, 2010). Consumer attitudes to sustainable production and to IPM are changing around the world, most notably for higher value products and food like wine and fresh fruit where pesticide residue issues are most sensitive. Current research shows the importance of traceability and clear labelling for consumers to support the higher prices of sustainably-produced premium products, This is particularly the case in 'green image' countries like New Zealand where the demand for production using ecological strategies is growing (Forbes *et al.*, 2009). Marketing strategies used by supermarkets now often incorporate the promotion of 'zero pesticide residues' or the use of 'fewer pesticide types' in crop protection, rather than 'pesticide-free' or 'produced with less pesticides'. Valuing key eco-services (ES) for agriculture, including biocontrol, pollination, and soil health and then conveying these ES values to consumers and policy-makers in an understandable form (Lawton, 1994; Costanza *et al.*, 1997; Landis *et al.*, 2000; Pilgrim *et al.*, 2010) remains an important challenge. However, this is a key process that will further assist the uptake of IPM research into agricultural practice.

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References

BEETLE report. 2009. *Long-term effects of genetically modified (GM) crops on health and the environment (including biodiversity): prioritization of potential risks and delimitation of uncertainties*. German Federal Office of Consumer Protection and Food Safety, BLaU-Umweltstudien and Genius GmbH, http://ec.europa.eu/environment/biotechnology/pdf/beetle_report.pdf.

Begg GS, Birch ANE, Iannetta PPM, Young MW, Squire GR. 2010. Engineering arable landscapes to balance the pros and cons of weeds. Proceedings of the IOBC/WPRS working group meeting 'Landscape management for functional biodiversity'. Cambridge (UK), 22 June–1 July, 2010. *IOBC/WPRS Bulletin* **56,** 13–16.

Benton TG, Vickery JA, Wilson JD. 2003. Farmland biodiversity: is habitat heterogeneity the key? *Trends in Ecology and Evolution* **18,** 182–188.

Birch ANE. 2008. Ecology of natural enemy–prey interactions: what can we learn for practical biocontrol? *Proceedings 23rd International Congress of Entomology,* Durban, South Africa, 6–12 July 2008, 121.

Birch ANE, Begg GS. 2010. The future central role of IPM in EU crop protection: how can ecological research be put into practice?

Proceedings Crop Protection in Northern Britain 23–24 February 2010, 9–14.

Birch ANE, Fenton B, Malloch G, Jones AT, Phillips MS, Harrower BE, Woodford JAT, Catley MA. 1994. Ribosomal spacer length variability in the large raspberry aphid, *Amphorophora ideai. Insect Molecular Biology* **3,** 239–245.

Birch ANE, Gordon SC, Fenton B, Malloch G, Mitchell C, Jones AT, Griffiths DW, Brennan RM, Graham J, Woodford JAT. 2004. Developing a sustainable IPM system for high value *Rubus* crops (raspberry, blackberry) for Europe. *Acta Horticulturae* **649,** 289–292.

Birch ANE, Griffiths BS, Caul S, Thompson J, Heckman LH, Krogh PH, Cortet J. 2007. The role of laboratory, glasshouse and field scale experiments in understanding the interactions between GM crops and soil ecosystems: a review of the ECOGEN project. *Pedobiologia* **51,** 251–260.

Birch ANE, Wheatley RE. 2005. GM pest-resistant crops: assessing environmental impacts on non-target organisms. Sustainability in agriculture. *Issues in Environmental Science and Technology* **21,** 31–57.

Champion GT, May MJ, Bennett S, *et al*. 2003. Crop management and agronomic context of the Farm Scale Evaluations of genetically modified herbicide-tolerant crops. *Philosophical Transactions of the Royal Society of London B* **358,** 1801–1818.

Cortet J, Griffiths BS, Bohanec M, *et al*. 2007. Evaluation of effects of transgenic Bt maize on microarthropods in a European multi-site experiment. *Pedobiologia* **51,** 207–218.

Costanza R, d'Arge R, de Groot R, *et al*. 1997. The value of the world's ecosystem services and natural capital. *Nature* **387,** 253–260.

Currano ED. 2009. Patchiness and long term change in early Eocene insect feeding damage. *Paleobiology* **35,** 484–498.

Daubeny HA. 1980. Red raspberry cultivar in British Columbia with special reference to pest response and germplasm exploitation. *Acta Horticulturae* **112,** 285–293.

Debeljak M, Squire GR, Kocev D, Hawes C, Young MW, Džeroski S. 2011. Analysis of time series data on agroecosystem vegetation using predictive clustering trees. *Ecological Modelling* doi:10.1016/j.ecolmodel.2010.10.021.

Dogimont C, Bendahmane A, Chovelon V, Biossot N. 2010. Host plant resistance to aphids in cultivated crops: genetic and molecular bases, and interactions with aphid populations. *Comptes Rendus Biologies* **333,** 566–573.

EFSA. 2006. Guidance document of the Scientific Panel on Genetically Modified Organisms for the risk assessment of genetically modified plants and derived food and feed. *The EFSA Journal* **99,** 1–100.

Engleman R. 2009. Population and sustainability. *Scientific American Earth 3.0* **19,** 22–29.

Eurostat. 2007. The use of plant protection products in the European Union. Data 1992–2003. Downloadable web source: *http://epp.eurostat.ec.europa.eu/cache/ITY_OFFPUB/KS-76-06-669/EN/KS-76-06-669-EN.PDF*.

Fagan LL, McLachlan A, Till CM, Walker MK. 2009. Synergy between chemical and biological control in the IPM of currant-lettuce aphid in Canterbury, New Zealand. *Bulletin of Entomological Research* **100,** 217–223.

Food and Agriculture Organization. 2002. International fund for agricultural development, world food program. 2002 Downloadable web source: ' *Reducing poverty and hunger, the critical role of financing for food, agriculture, and rural development*'. www.fao.org/docrep/003/y6265e/y6265e00.HTM.

Food and Agriculture Organization. 2009. Downloadable web source: ' *The state of food insecurity in the world*'. ftp://ftp.fao.org/docrep/fao/012/i0876e/i0876e.pdf.

Forbes SL, Cohen DA, Cullen R, Wratten SD, Fountain J. 2009. Consumer attitudes regarding environmentally sustainable wine: an exploratory study of the New Zealand marketplace. *Journal of Cleaner Production* **17,** 1195–1199.

Firbank LG, Heard MS, Woiwod IP, *et al*. 2003. An introduction to the Farm Scale evaluations of genetically modified herbicide-tolerant crops. *Journal of Applied Ecology* **40,** 2–16.

Fried G, Norton LR. 2008. Environmental and management factors determining weed species and diversity in France. *Agriculture Ecosystems & Environment* **128,** 68–76.

Gregory PJ, Johnson SN, Newton AC, Ingram JSI. 2009. Integrating pests and pathogens into the climate change/food security debate. *Journal of Experimental Botany* **60,** 2827–2838.

Griffiths BS, Caul S, Thompson JT, Birch ANE, Cortet J, Andersen MN, Henning Krogh PH. 2007. Microbial and microfaunal community structure in cropping systems with genetically modified plants. *Pedobiologia* **51,** 195–206.

Hawes C, Begg GS, Squire GR, Iannetta P. 2005. Individuals as the basic accounting unit in studies of ecosystem function: functional diversity in *Capsella* (shepherd's purse). *Oikos* **109,** 521–534.

Hawes C, Haughton AJ, Bohan DA, Squire GR. 2009. Functional approaches for assessing plant and invertebrate abundance patterns in arable systems. *Basic and Applied Ecology* **10,** 34–42.

Heard MS, Hawes C, Champion GT, *et al*. 2003. Non-crop plants in fields with contrasting conventional and genetically modified herbicide-tolerant crops. 1. Main effects of treatments. *Philosophical Transactions of the Royal Society of London B* **358,** 1819–1832.

Heinrichs EA, Maredia KM, Mohankumar S. 2009. Future of IPM a worldwide perspective. In: Radcliffe EB, Hutchison WD, Cancelado RE, eds. *Integrated pest management. Concepts, tactics, strategies and case studies*. Cambridge University Press, 506–522.

Hillier J, Hawes C, Squire GR, Hilton A, Wale S, Smith P. 2009. The carbon footprints of food crop production. *International Journal of Agricultural Sustainability* **7,** 107–118.

Hutchison WD, Burkness EC, Mitchell PD, *et al*. 2010. Area-wide suppression of European corn borer with Bt maize reaps savings to non-Bt maize growers. *Science* **330,** 222–225.

Iannetta P, Begg G, Hawes C, Squire GR. 2007. Variation in *Capsella* (Shepherd's Purse): an example of intra-specific functional diversity. *Physiologia Plantarum* **129,** 542–554.

Iannetta PPM, Begg GS, Valentine TA, Wishart J. 2010. INSIGHTS: sustainable disease control using weeds as indicators: *Capsella bursa-pastoris* and Tobacco Rattle Virus. *Weed Research* **50,** 511–514.

Jongejans E, Skarpaas O, Shea K. 2008. Dispersal, demography and spatial population models for conservation and control management. *Perspectives in Plant Ecology, Evolution and Systematics* **9,** 153–170.

Jonsson M, Wratten SD, Landis DA, Gurr GM. 2008. Recent advances in conservation biological control of arthropods by arthropods. *Biological Control* **45,** 172–175.

Karley, AJ, Hawes C, Iannetta PPM, Squire GR. 2008. Intraspecific variation in *Capsella bursa-pastoris* in plant quality traits for insect herbivores. *Weed Research* **48,** 147–156.

Khan ZR, Midega CAO, Bruce TJA, Hooper AM, Pickett JA. 2010. Exploiting phytochemicals for developing a 'push–pull' crop protection strategy for cereal farmers in Africa. *Journal of Experimental Botany* **61,** 4185–4196.

Koul O, Cuperus GW, Elliot N, eds. 2008. *Area-wide pest management: theory to implementation*. UK: CAB International, 560–572.

Landis DA, Wratten SD, Gurr GM. 2000. Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology* **45,** 175–201.

Lawton JH. 1994. What do species do in ecosystems? Oikos **71,** 367–374.

Lu YL, Wu K, Jiang Y, Xia B, Li P, Feng H, Wyckhuys KAG, Guo Y. 2010. Mirid bug outbreaks in multiple crops correlated with widescale adoption of Bt cotton in China. *Science* **328,** 1151–1154.

May MJ, Champion GT, Dewar AM, Qi A, Pidgeon JD. 2005. Management of genetically modified herbicide-tolerant sugar beet for spring and autumn environmental benefit. *Proceedings of the Royal Society B* **272,** 111–119.

Messean A, Squire G, Perry J, *et al*. 2009. Sustainable introduction of GM crops into European agriculture: a summary report of the FP6 SIGMEA research project. *OCL* **16,** 37–51.

Nassauer JI, Opdam P. 2008. Design in science: extending the landscape ecology paradigm. *Landscape Ecology* **23,** 633–644.

Newton AC, Begg GS, Swanston S. 2009. Deployment of diversity for enhanced crop function. *Annals of Applied Biology* **154,** 309–322.

Nicholls CI, Altieri MA. 2004. The agro-ecological bases of ecological engineering for pest management. In: Gurr GM, Wratten SD, Altieri MA, eds. *Ecological engineering for pest management*. Melbourne: CSIRO Publishing (Australasian publisher); Wallingford, UK: CAB International (European Publisher); Ithaca, USA: Cornell University Press (Americas publisher), 33–54.

Oerke E-C. 2006. Crop losses to pests. *Journal of Agricultural Science* **144,** 31–45.

Orre GUS, Wratten SD, Jonsson M, Hale RJ. 2009. Effects of an herbivore-induced plant volatile on arthropods from three trophic levels in brassicas. *Biological Control* **53,** 62–67.

Ostfeld RS, Glass GE, Keesing F. 2005. Spatial epidemiology: an emerging (or re-emerging) discipline. *Trends in Ecology and Evolution* **20,** 328–336.

Parmesan C, Root TL, Willig WR. 2000. Impacts of extreme weather and climate on terrestrial biota. *Bulletin of the American Meteorological Society* **81,** 443–450.

Pickett JA, Hamilton ML, Hooper AM, Khan ZR, Midega CAO. 2010. Companion cropping to manage parasitic plants. *Annual Review of Phytopathology* **48,** 161–177.

Pilgrim ES, Macleod CJA, Blackwell MSA, *et al*. 2010. Interactions amongst agricultural production and other ecosystem services delivered from European temperate grassland systems. *Advances in Agronomy* **109,** 117–154.

Plantegenest M, Le May C, Fabre F. 2007. Landscape epidemiology of plant diseases. *Journal of the Royal Society Interface* **4,** 963–972.

Pretty J. 2005. Sustainability in agriculture: recent progress and emergent challenges. Sustainability in agriculture. *Issues in Environmental Science and Technology* **21,** 1–15.

Pretty J. 2009. *Can ecological agriculture feed nine billion people?* Online publication: www.monthlyreview.org/091123pretty.php

Rahman T, Roff MNM, Ghani IBA. 2010. Within-field distribution of *Aphis gossypii* and aphidophagous lady beetles in chili, *Capsicum annuum. Entomologia Experimentalis et Applicata* **137,** 211–219.

Robertson GW, Griffiths DW, Woodford JAT, Birch ANE. 1994. Changes in the chemical composition of volatiles released by the flowers and fruits of the raspberry cv. Glen Prosen. *Phytochemistry* **38,** 1175–1179.

Rodríguez JP, Beard Jr TD, Bennett EM, Cumming GS, Cork S, Agard J, Dobson AP, Peterson GD. 2006. Trade-offs across space, time, and ecosystem services. *Ecology and Society* **11,** 28.

Roschewitz I, Gabriel D, Tscharntke T, Thies C. 2005. The effects of landscape complexity on arable weed species diversity in organic and conventional farming. *Journal of Applied Ecology* **42,** 873–882.

Sargent DJ, Fernández-Fernández F, Rys A, Knight VH, Simpson DW, Tobutt KR. 2007. Mapping of A_1 conferring resistance to the aphid *Amphorophora idaei* and *dw* (dwarfing habit) in red raspberry (*Rubus idaeus* L.) using AFLP and microsatellite markers. *BMC Plant Biology* **7,** 15–24.

Squire GR, Brooks DR, Bohan DA, *et al*. 2003. On the rationale and interpretation of the farm-scale evaluations of genetically-modified herbicide-tolerant crops. *Philosophical Transactions of the Royal Society of London B* **358,** 1779–1800.

Squire GR, Hawes C, Begg GS, Young MW. 2009. Cumulative impact of GM herbicide-tolerant cropping on arable plants assessed through species-based and functional taxonomies. *Environmental Science and Pollution Research* **16,** 85–94.

Squire GR, Hawes C, Bohan DA, *et al*. 2005. *Biodiversity effects of the management associated with GM cropping systems in the UK*. London, UK: Defra.

Squire GR, Young M, Karley A. 2010. Comparative ecological effects of GM and other innovations in maritime arable-grass production systems. In: Breckling B, Reuter H, Verhoeven R, eds. *Implications of GM-crop cultivation at large spatial scales*. Frankfurt, Germany: Peter Lang.

Stern VM, Smith RF, van den Bosh R, Hagen KS. 1959. The integration of chemical and biological control of the spotted alfalfa aphid (the integrated control concept). *Hilgardia* **29,** 81–101.

Straub CS, Finke DL, Snyder WE. 2008. Are the conservation of natural enemy biodiversity and biological control compatible goals? *Biological Control* **45,** 225–237.

Tank JL, Rosi-Marshall EJ, Royer TV, Whiles MR, Griffiths NA, Frauendendorf TC, Treering DJ. 2010. Occurrence of maize detritus and transgenic insecticidal protein (Cry1Ab) within the stream network of an agricultural landscape. *Proceedings of the National Academy of Sciences, USA* **107,** 17645–17650.

Tilman D, Fargione J, Wolff B, D'Antonio C, Dobson A, Howarth R, Schindler D, Schlesinger WH, Simberloff D, Swackhamer D. 2001. Forecasting agriculturally driven global environmental change. *Science* **292,** 281–284.

Toorop PE, Begg GS, Wishart J, Iannetta PPM. 2008. Germination characters and myxospermy of shepherds purse (*Capsella bursa-pastoris* (L.) Medic) time to flowering variants. Abstract from the 9th Conference on Seed Biology, Olsztyn, Poland, 6–11 July 2008*. Polish Journal of Natural Sciences* Supplement **5**,101.

Tscharntke T, Bommarco R, Clough Y, Crist TO, Kleijn D, Rand TA, Tylianakis JM, van Nouhuys S, Vidal S. 2007. Conservation biological control and enemy diversity on a landscape scale. *Biological Control* **43,** 294–309.

Tscharntke T, Sekercioglu CH, Dietsch TV, Sodhi NS, Hoehn P, Tylianakis JM. 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. *Ecology* **89,** 944–951.

Vandermeer J. 1989. *The ecology of intercropping*. London, UK: Cambridge University Press.