

***Bt* crops: Predicting effects of escaped transgenes on the fitness of wild plants and their herbivores**

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One prominent concern about genetically modified crops is the possibility of environmental impacts from the movement of fitness-enhancing traits to wild plant populations. Decisions to deregulate *Bt* crops in the USA have relied strongly on arguments that these crops will not interbreed with wild relatives in the permitted growing regions. Limited attention therefore has been directed to analyses of the consequences of gene flow. To provide a transparent evaluation process for risks associated with insecticidal transgene escape, we crafted a series of questions designed to guide this aspect of the risk assessment. We then explored the current knowledge base available for answering such risk-related questions for three *Bt* crops (cotton, rapeseed, and rice). First, we generated a list of wild relatives of these crops. A definitive list of potential transgene recipients is not yet possible for some crops. Sufficient data are not available for some crops to eliminate certain related plant species from consideration of fertile hybrid formation, thus making lists for these crops subject to speculation. Second, we queried the HOSTS database (UK) to obtain a worldwide listing of lepidopteran species that feed on these crops and their wild relatives, and to determine the host range of the larvae. To our knowledge, this list of 502 lepidopteran species is the first such list published for these crops and wild crop relatives. Third, we used a data set maintained by the Canadian Forest Service to assess *Bt* toxin susceptibility for these lepidopterans. Only 3% of those species have been tested for susceptibility; and the literature suggests that generalizations about susceptibility among taxa are difficult due to the variability within families. Fourth, we consulted the literature to interpret what is known about the ability of lepidopterans to regulate plant fitness or invasiveness. We could not eliminate the possibility of ecological release due to plant resistance against lepidopterans. In fact, there is strong experimental evidence that lepidopteran herbivores do limit the distribution and/or abundances of at least some wild plant species. Neither could we eliminate the possibility that non-target lepidopterans might have important functions in the ecosystem as pollinators or alternate hosts to natural enemies of pest species. This study suggests that crucial data are lacking for the development of a credible scientific basis to confirm or deny environmental risks associated with the escape of *Bt* transgene constructs to wild relatives. Given the absence of information on the identity, level of susceptibility, and ecological roles of lepidopterans exploiting specific wild relatives of *Bt* crops, we suggest that new efforts be directed to assessing possible consequences of lepidopteran mortality on resistant wild relatives.

Keywords: *Bt* cotton / *Bt* rapeseed / *Bt* broccoli / *Bt* rice / superweed / risk assessment / biosafety / Lepidoptera / herbivores / insect-resistant crops / host plant database

INTRODUCTION

A wide range of crop plants and trees have been transformed with genes derived from the soil bacterium *Bacillus thuringiensis* (*Bt*) to express insecticidal proteins (insect-resistant *Bt* plants), including corn, soybean, rice,

tomato, broccoli, coffee, poplar, and Loblolly pine. Whereas the adoption of *Bt* plants constitutes one of the most common uses of transgenic plants in agriculture, the environmental benefits and risks remain an issue of

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contention. *Bt* plants have been promoted as beneficial to the environment because (1) the resistance mechanism is specific, affecting few but the target taxa and (2) *Bt* based host plant resistance allows for reduced pesticide use (Betz et al., 2000; Peferoen, 1997; Phipps and Park, 2002). Both taxon-specific pesticidal properties and reduced pesticide usage are key components of integrated pest management strategies designed to promote biological control through the conservation of natural enemies (Barbosa, 1998; Hull and Beers, 1985; Mullin and Croft, 1985). Researchers have called for a variety of assessments, to quantify each of the environmental benefits of *Bt* crops, including (1) adequate tests of lethal, sub-lethal, direct, and indirect effects of *Bt* toxins in plants on non-target and/or beneficial organisms (Hilbeck, 2002; Obrycki et al., 2001; Pilson and Decker, 2002; Saxena et al., 1999; Srinivasan and Babu, 2001), (2) measures of actual pesticide reduction with *Bt* plants, whose range of pests is broader than lepidopterans (Benbrook et al., 1996; Wolfenbarger and Phifer, 2000), and (3) alternative standard comparisons beyond *Bt*- and non-*Bt*-isolines under conventional crop management practices to assess environmental benefits, such as performance of the crop under organic or biological management practices (NRC, 2002; Peterson et al., 2000; Wolfenbarger and Phifer, 2000). Even more common are calls for the assessment of environmental impacts involving gene escape from *Bt* plants (Hails, 2000; Royal Society of Canada, 2001). *Bt* toxin based pest resistance is a trait that, should it escape (be transferred to wild plants), could also protect recipient plant populations from damage by susceptible herbivores. Traits such as insect resistance are of special concern because they may relieve a wild plant of some of its natural constraints to population growth. Such an ecological release may increase the population densities or range of occurrence of that plant, thereby increasing weediness or creating a weedy condition (Bergelson and Purrington, 2002; Klinger, 2002; Snow and Palma, 1997; Snow et al., 2003). Increased fitness, competitive ability, and invasiveness of a crop's wild relatives has been a primary concern of research ecologists and regulatory agencies as transgenes conferring novel forms of pest resistance have been incorporated into a range of cultivated plant varieties (Colwell et al., 1985; Darmency, 1994; Hails, 2000; Hoffman, 1990; Kareiva et al., 1994; Louda, 1999; Royal Society of Canada, 2001; Tiedje et al., 1989).

We consider the specific case of the novel resistance trait of *Bt* endotoxin expression against lepidopterans and the potential of such a trait, if it should be expressed in wild relatives of crop plants, to cause a change in weed

status of those wild plants. If lowered herbivory on a strongly resistant host plant leads to increased fitness of that plant through various avenues, including increased photosynthetic capacity, vigor, seed output and seed weight, these changes might result in greater levels of invasiveness. Greater levels of invasiveness result in problems such as increased revenues for weed control, displacement of desired or native vegetation, reduced crop yields, loss of refugia for susceptible herbivores, and/or loss of biodiversity through increased mortality of non-target lepidopterans. Whether or not such potential hazards are realized, however, depends on a series of events, each with its own conditions and levels of uncertainty (Bergelson and Purrington, 2002; Jenczewski et al., 2003). These events include (1) the successful transfer of a transgenic trait to a particular wild relative of the crop; (2) an increase of the genetic construct and the resistant phenotype in the recipient population; and (3) some resulting hazard associated with that trait in the environment (such as those listed above). While significant research on the rate and success of transfer of transgenic traits to wild relatives has been achieved for several crop-wild relative combinations (*e.g.* Chèvre et al., 2000; Jørgensen and Andersen, 1994; Lefol et al., 1997; Messeguer et al., 2001; Mikkelsen et al., 1996; Song et al., 2003), less research has focused on the subsequent hazards of such gene flow.

Critical questions for identifying potential hazards of lepidopteran-resistant *Bt* crops and assessing the probabilities of such an effect occurring include: Which wild plant populations could receive transgenes from these crops through pollen transfer? Which lepidopterans feed on these host plants? What subset of these lepidopterans is susceptible to the endotoxins produced by the related *Bt* crop? Do lepidopterans play a role in regulating those plant populations? Which plants, under what circumstances, when released from herbivory, will exhibit higher fitness? Over time, will the plant population spread or become invasive? What are other possible effects of *Bt* toxins, including direct effects on lepidopteran population dynamics (for example, pollinators of other plant species and reduction of parasitoid reservoirs due to high larval mortality) and direct or indirect effects on other organisms?

Our main objective here is to demonstrate a science-based approach to environmental biosafety assessment for transgene escape from transgenic, insect-resistant crops, and to illustrate the state of knowledge and resources currently available to answer ecological questions relevant to that assessment. We offer a flow diagram (Fig. 1) that incorporates such questions in a

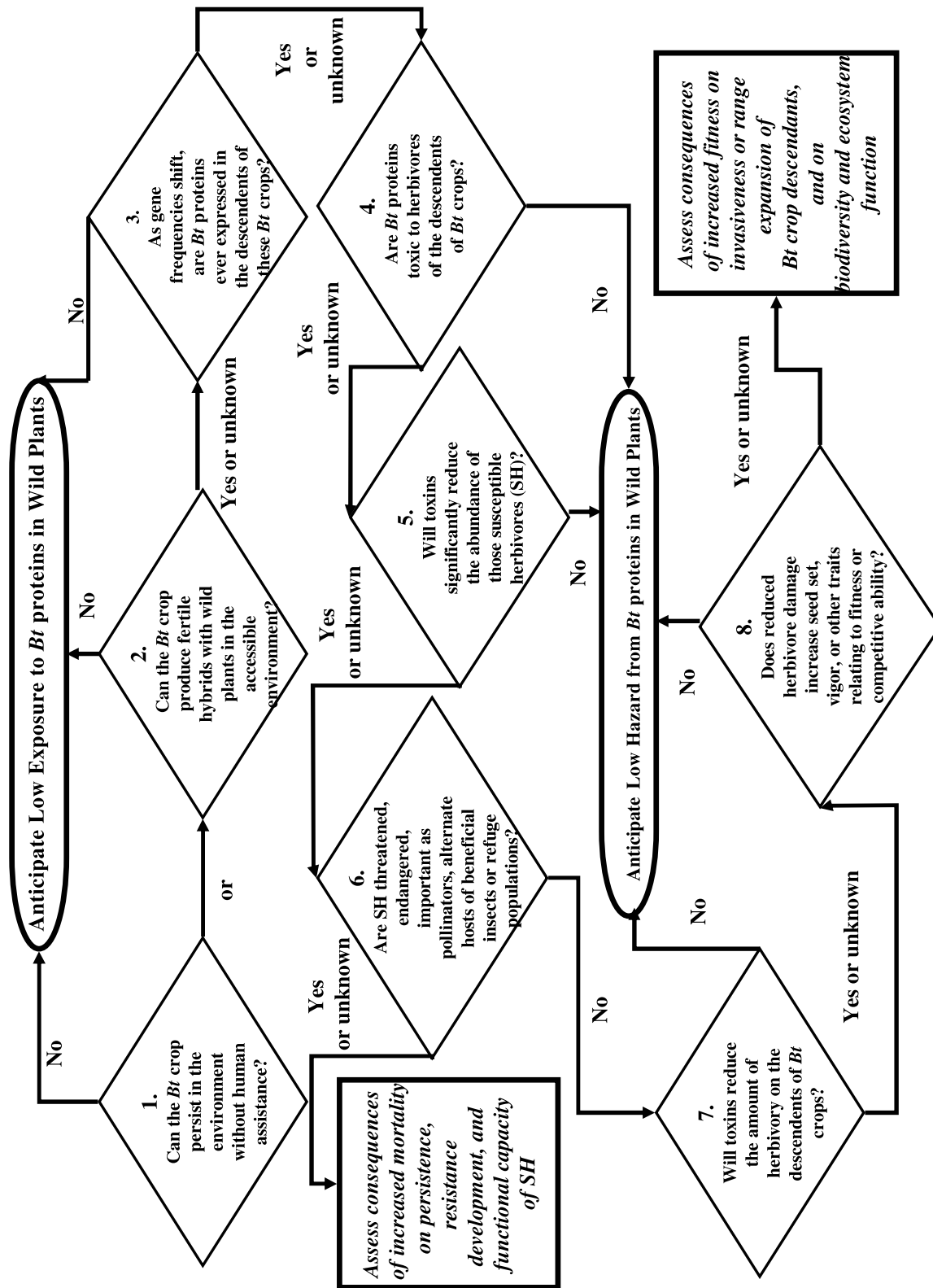


Figure 1. Step-by-step flow diagram for assessing ecological questions related to the risks of *Bt* transgene escape into wild populations of the crop or its relatives (modified from Letourneau et al., 2002).

Table 1. Wild relatives of selected *Bt* crops. Sexual compatibility was determined by forced pollinations unless otherwise noted.

<i>Brassica napus</i> (rapeseed, canola) <i>Brassica rapa</i> (previously <i>B. campestris</i>) ^{3,6} <i>Brassica nigra</i> ⁴ <i>Brassica juncea</i> ^{2, 6} <i>Raphanus raphanistrum</i> ² <i>Raphanus sativus</i> ² <i>Brassica oleracea</i> ^{9, 10} <i>Sinapis arvensis</i> (prev. <i>Brassica kaber</i>) ⁸ <i>Hirschfeldia incana</i> ² <i>Cakile edentula</i> ⁷ <i>Cakile maritima</i> ⁷ <i>Cardamine californica</i> ⁷	<i>Oryza sativa</i> (rice) <i>Oryza sativa</i> and <i>Oryza nivara</i> * (wild red rice) ^{1,3,5,6} <i>Oryza rufipogon</i> ^{3, 5} <i>Oryza longistaminata</i> ⁴ <i>Oryza glaberrima</i> ⁴ <i>Oryza barthii</i> ^{9, 10} * Synonym
<i>Brassica oleracea</i> (broccoli, cabbage, cauliflower, brussels sprouts, collards, etc.) <i>Brassica napus</i> ² <i>Brassica rapa</i> ^{9, 10}	<i>Gossypium hirsutum</i> (cotton) <i>Gossypium barbadense</i> ^{1, 2} <i>Gossypium tomentosum</i> ² <i>Gossypium barbadense darwinii</i> ⁷ <i>Gossypium mustelinum</i> ⁷

¹ Cross-compatible; ² fertile hybrids obtained; ³ high rates of hybridization reported; ⁴ low rates of hybridization reported, high sterility of hybrids; ⁵ USA Federal Noxious Weed List; ⁶ hybrids occur naturally in the field; ⁷ never tested for hybridization with crop; ⁸ no hybrids obtained (Bing, 1991); ⁹ ancestral crosses but no evidence of recent hybridization; ¹⁰ gene transfer via "bridging" only; whereas no hybrids between this relative and the crop are expected, gene transfer from the crop to this wild relative could occur via another wild relative which is interfertile with the crop and with this relative.

step-by-step assessment. This assessment differs from some regulatory practices in risk assessment in that it lays the burden of evidence on biosafety rather than on proving harm. To examine the questions posed in Figure 1 for *Bt* rice, *Bt* cotton, and *Bt* rapeseed we queried databases and synthesized data from published studies. These crops represent three distinct plant families grown presently as non-transformed cultivars in many countries of the world, and as transgenic cultivars in the case of cotton. Although we focus on lepidopteran-resistant *Bt* crops, we suggest that many of the questions and data we present could be adapted readily to assessments of *Bt* crops resistant to Coleoptera, Diptera or a broader range of pest taxa.

Potential for gene flow between *Bt* crops and wild relatives

All commercialized *Bt* crops either exist in the wild themselves or hybridize with wild relatives somewhere in their range (Ellstrand et al., 1999; Snow and Palma, 1997). For hybridization to occur, the plants must be close enough to each other, in both space and phenological time, for pollen or pollen vectors to move between flowering plants (Ellstrand et al., 1999). The compilation of a

comprehensive list of plant species potentially able to produce fertile hybrids with *Bt* crop plants constitutes the first step in determining the potential exposure of the transgene in an assessment of risk associated with gene flow (Fig. 1, questions 1 and 2) (Neeser, 1999; NRC, 2000). For the purpose of this study, we have constructed a list of wild relatives of rapeseed, cotton and rice (Tab. 1), which, though not comprehensive, includes those species that are known to produce fertile offspring as well as a subset of other related plant species. This subset of other plants represents species that are potentially wild relatives of interest due to phylogenetic proximity, but for which little or nothing is known about their actual potential for producing fertile hybrids with related *Bt* crops. That is, neither barriers to successful hybridization nor results of experimental attempts have been documented. The inclusion of such examples of wild relatives for which there is little information is based on two known phenomena: (1) rare events of successful hybridization that may not be discovered without active experimentation and (2) the production of fertile hybrids through intermediate bridging.

Bridging is an avenue for transgene movement from a crop into a wild plant population, even when the wild

plant species is sexually incompatible with the transgenic crop. For example, *Brassica oleracea* (cole crops such as broccoli, cabbage, and kale, $CC\ 2n = 18$) is not known to cross with its various related weed species, including *B. rapa* (field mustard, $AA\ 2n = 20$). However, *B. oleracea* can form a fertile hybrid with *Brassica napus* (rapeseed, $AACC\ 2n = 38$) (Tab. 1). Those resulting hybrids can then cross with *B. rapa*, an important and widespread weed (Hauser et al., 1998; Jørgensen et al., 1996; Snow et al., 1999). Indeed, *B. napus* evolved from ancestral, natural crosses between the diploid species *B. oleracea* and *B. rapa*. Therefore, we include *B. oleracea* (genetically engineered broccoli or cabbage) and *B. rapa* as possible interbreeding species even though fertile hybrids between these species have not been produced in recent times (U, 1935). Because of existing knowledge gaps for some crops, lists of their potential recipient species can be expanded or contracted according to different baseline assumptions.

The evidence supporting decisions on whether or not a particular plant species is considered a possible source of spontaneous crop-wild hybrids should be provided as a transparent part of the environmental assessment process. If the production of fertile crop-wild hybrids is possible, but expected to be an extremely rare occurrence, it can be viewed in two ways: (1) as an acceptably low risk or (2) as an eventual certainty that will occur given enough time and space. We suggest that even the former viewpoint should not be a reason to dismiss further consideration of the consequences of gene flow. Any possibility, however remote, of transgene introgression into wild populations, should be accompanied by an evaluation of its possible consequences (Fig. 1).

Consequences of transgene expression in wild relatives of crops

Hazards associated with the movement of *Bt* transgenes to wild relatives of *Bt* crops could include increased weediness of the wild relatives; however, population decline of the wild relative is also conceivable should the transgene be detrimental in some way (Bergelson and Purrington, 2002; Elstrand et al., 1999). Other potential hazards include detrimental effects on non-target organisms if the proteins are expressed sufficiently and if these species are sufficiently challenged by the toxic proteins (Fig. 1, questions 3 and 4). We emphasize in our discussion effects on susceptible lepidopterans feeding on wild plant recipients of *Bt* transgenes. However, a wider range of organisms will be exposed to *Bt* proteins that persist in the soil, pollen, and herbivores of these plants (Fig. 1,

questions 4–6). The detrimental consequences of mortality in endangered species are obvious, but even non-target moths or butterflies are harmed, unwanted indirect effects may occur (such as lower pollination rates of a rare plant or reduction of alternate hosts for natural enemies). To assess potential hazards of *Bt* toxin in the tissues of wild relatives, a reasonable starting point is an accurate list of the herbivore species that might be exposed to these toxins (Fig. 1, questions 4–6). We queried The Natural History Museum's HOSTS database to create lists of Lepidoptera known to feed on plants in our sample list of *Bt* crops and wild relatives.

The Natural History Museum's HOSTS database (described by Robinson, 1999) is a compilation of, currently, 175 000 host plant records of the world's Lepidoptera drawn from more than 1600 published, manuscript and electronic sources. An abbreviated version is available online: <http://www.nhm.ac.uk/entomology/hostplants/>, and published compilations of HOSTS data are available for the "Oriental" region (Robinson et al., 2001) and North America (Robinson et al., 2002a, 2002b).

Although extensive, and perhaps surprisingly diverse, Appendix 1 does not list all of the lepidopteran species that may be of interest as non-target herbivores on our sample of *Bt* crops and wild relatives. HOSTS contains information culled from both the economic and non-applied entomological literatures, but records at least one host plant for only 19% of the world's described species of Lepidoptera. Thus, it provides a broad and credible coverage not available from any other source, yet it is still not comprehensive for listing all of the lepidopteran species that could be affected by escaped transgenes.

These difficulties in knowing the potential breadth of exposure to *Bt* crop toxins, even for a relatively well-known order of insects, create a level of uncertainty for detailed risk assessment. Some groups will be under-represented because knowledge of different groups of Lepidoptera and richness of different categories of data vary widely (Beccaloni, unpubl.). For example, the database includes host plants for 42% of ~875 species of Nepticuloidea, and for 69% of ~2000 species of Gracillarioidea because these groups are often collected by rearing. In contrast, host plants for only 9% of the 21 900 Geometroidea and 13% of the 15 900 Pyraloidea are known. These problems may be even more pronounced for microlepidopteran species.

Some plants (including some *Bt* crop relatives) and geographic regions (accessible environments for *Bt* crops and transgenes) are expected to be under-reported. For HOSTS, abstracting of literature has been extensive and

Table 2. Total number of Lepidoptera species (subspecific categories pooled) with larvae recorded as feeding upon *Bt* modified or closely related plants. Data from The Natural History Museum's HOSTS database (see Robinson, 1999).

Cruciferae	<i>Brassica juncea</i>	25
	<i>Brassica napus</i>	26
	<i>Brassica nigra</i>	28
	<i>Brassica oleracea</i>	123
	<i>Brassica oleracea acephala</i>	4
	<i>Brassica oleracea botrytis</i>	15
	<i>Brassica oleracea bullata</i>	7
	<i>Brassica oleracea capitata</i>	58
	<i>Brassica oleracea gemmifera</i>	7
	<i>Brassica oleracea gongylodes</i>	2
	<i>Brassica oleracea italica</i>	4
	<i>Brassica rapa</i>	52
	<i>Cakile edentula</i>	4
	<i>Cakile maritima</i>	7
	<i>Cardamine californica</i>	2
	<i>Hirschfeldia incana</i>	9
	<i>Raphanus raphanistrum</i>	9
<i>Raphanus sativus</i>	49	
<i>Sinapis arvensis</i>	6	
Gramineae	<i>Oryza barthii</i>	0
	<i>Oryza glaberrima</i>	2
	<i>Oryza longistaminata</i>	0
	<i>Oryza nivara</i>	0
	<i>Oryza rufipogon</i>	0
	<i>Oryza sativa</i>	292
Malvaceae	<i>Gossypium barbadense</i>	31
	<i>Gossypium barbadense darwinii</i>	0
	<i>Gossypium hirsutum</i>	22
	<i>Gossypium mustelinum</i>	0
	<i>Gossypium tomentosum</i>	2

approaches practical limits for the "Oriental" region, North America, Western Europe and the Afrotropical region, whereas coverage of Central and South America, Asia excluding Western Europe, and Australasia is less comprehensive. Disproportionately fewer host records have been recorded from wild plants than from crop plants because crop pests are preferentially studied. Also, it is rare to find host plant records that cite the subspecies or variety of the plant, which makes it particularly difficult to retrieve records for, say, *Brassica oleracea gongylodes* in contrast to *Brassica oleracea*. In addition,

misidentification, synonymy, and other potential sources of error are manifold and parallel those encountered in records of host-parasite relationships (Fitton et al., 1988).

Appendix 1 lists 502 lepidopteran species recorded as feeding on cotton, cole crops, rice and their wild relatives, together with a measure of their reported host plant range and geographical distribution. The total number of species recorded as feeding on each of the host plants queried varies from 0 to 292 (Tab. 2). To our knowledge, no such inventory of the herbivores on these plants has

been published previously, making it difficult even to conceive of the number of non-target lepidopterans potentially to be exposed to *Bt* toxins in the crops and in their wild relatives if the trait were to be transferred.

To approach the question of hazards to lepidopterans, further searches were made of HOSTS to determine how many of these lepidopteran species are potentially dependent upon only one of these hostplants for their survival (Tab. 3). Despite inherent limitations (see Letourneau et al., 2002), HOSTS can provide initial lists of Lepidoptera and some estimate of how dependent these herbivores are on the host plant in question. We consider all the *Brassica* species listed to be fairly well studied because they are crop-plants. Of the 180 Lepidoptera species recorded from these plants, 41% occur on more than one *Brassica* species (Tab. 4). Among those species with multiple hosts, most combinations are represented, suggesting that, to a caterpillar, one *Brassica* is much the same as another. Of the 10 species listed as feeding on *Cakile*, 60% feed also on other genera of Brassicaceae. For *Cardamine*, *Hirschfeldia*, *Raphanus* and *Sinapis*, 100, 67, 81 and 67% respectively of their herbivores feed also on other crucifer genera and their diet range always includes at least one *Brassica* crop species.

In the Poaceae (Tab. 5), three of four species recorded from non-crop plants feed also on the related crop plant. Of 44 species feeding on *Gossypium* (Tab. 6), 43% of the 23 species that feed on its non-economic relatives feed also on *G. barbadense*. From the limited records available we may speculate that 40–100% of the herbivores recorded from the non-economic relatives of crop plants feed also on the crop plant species. The inference seems fair that a similar proportion of the species feeding on the crop plant might feed on the non-crop relatives as well (given geographic feasibility), but sufficient data simply have not been recorded.

The potential transfer of transgenic insecticidal traits to close relatives of crop plants may have implications for biodiversity (Fig. 1, questions 5 and 6). This is especially true for crops with very high acreages of *Bt* varieties because of the spatial exclusion and swamping of edible host plants with palatable, but continuously toxic ones. Moths and butterflies that are host-specific, and whose host plants inherit the ability to produce lethal toxins, will experience local extinctions (or become resistant). Under-recording no doubt inflates artificially the impression of widespread monophagy within the Lepidoptera (Letourneau et al., 2002). However, of 18 503 Lepidoptera species for which we have at least one host plant record, almost half (9062) are recorded from just a single

host plant species (Robinson, 1998). In Table 3 we list Lepidoptera taxa that are recorded as feeding *only* on the crop-plant (or near-relative) genera and which are endemic to the same geographical region as that in which the crop plant (and its putative progenitors) originated. For the plant genera dealt with here, 80 Lepidoptera species *appear* to have a host range that is restricted to that genus. If locally available hosts were to obtain the insect-resistance trait, there could be several types of consequences, from the extirpation of these potentially host-specific, non-target lepidopteran species to the hastened development of resistance in crop pests. The spread of an insect-resistance trait in formerly susceptible wild relatives of crop plants would eliminate a natural “refuge” that serves to maintain susceptible pest lepidopterans in the target population (Alstad and Andow, 1995; Andow, 2002).

Susceptibility of lepidopteran species to *Bt* toxins

One general protocol for assessing the effects of a transgene coding for *Bt* proteins in a wild relative of a crop plant would be to determine directly if any of the herbivores that feed on that plant are susceptible to the toxin (produced in response to the *cry* gene in question). If the herbivores are not susceptible to the *Bt* proteins, then neither the transgenic offspring nor the herbivore is likely to experience population level changes due to the insect resistance trait *per se*, and risk assessment research efforts might be directed elsewhere (Fig. 1, questions 4, 5 and 7). Typically, research efforts have emphasized testing of major target pests or a known susceptible insect rather than a range of lepidopterans that occur either on target host plants or in geographic areas of toxin introduction. We are aware of no systematic measurement of mortality rates for the hundreds of lepidopterans recorded as feeding on *Bt* crops and their relatives.

To determine which of the species recorded in Appendix 1 are susceptible to *Bt* endotoxins, we consulted a comprehensive database of published toxicity studies for *Bt* maintained by the Canadian Forest Service (van Frankenhuyzen K. and Nystrom C., “The *Bacillus thuringiensis* toxin specificity database”, (1999), <http://www.glf.cfs.nrcan.gc.ca/bacillus>). As of January 2001, approximately 3% of the 502 lepidopterans known to use rapeseed, cotton, rice, and wild relatives of these *Bt* crops had been tested for *Bt* susceptibility (commercially available proteins) as documented in published studies. Specifically, of all the lepidopteran species listed in Appendix 1, susceptibility data are available on the following

Table 3. Lepidoptera species (subspecific categories pooled) with a recorded host range of only one plant genus within which *Bt* manipulation has occurred and which are potentially at risk of extirpation if no alternative host exists.

Arctiidae ¹	<i>Amata huebneri</i> Boisduval	or	<i>Oryza</i>
	<i>Cretonotos punctivitta</i> Walker	af	<i>Oryza</i>
	<i>Estigmene senegalensis</i> Rothschild	af	<i>Oryza</i>
	<i>Schistophleps bipuncta</i> Hampson	or	<i>Oryza</i>
	<i>Spilosoma scortilla</i> Wallengren	af	<i>Oryza</i>
	<i>Thumatha fuscescens</i> Walker	or	<i>Oryza</i>
Gelechiidae	<i>Athrips studiosa</i> Meyrick	or	<i>Oryza</i>
	<i>Helcystogramma nr. malacogramma</i> Meyrick	af	<i>Oryza</i>
	<i>Pityocona xeropsis</i> Meyrick	or	<i>Oryza</i>
Geometridae	<i>Pamphlebia rubrolimbraria</i> Guenée	or	<i>Oryza</i>
Gracillariidae	<i>Phyllonorycter triarcha</i> Meyrick	af; or	<i>Gossypium</i>
Hesperiidae	<i>Ampittia dioscorides</i> Fabricius	or	<i>Oryza</i>
	<i>Baoris pagana</i> de Nicéville	or	<i>Oryza</i>
	<i>Parnara poutieri</i> Boisduval	af	<i>Oryza</i>
	<i>Potanthus tropica</i> Plötz	or	<i>Oryza</i>
	<i>Prosopalpus styła</i> Evans	af	<i>Oryza</i>
Lymantriidae	<i>Laelia fasciata</i> Moore	or	<i>Oryza</i>
	<i>Laelia rosea</i> Schaus & Clement	af	<i>Oryza</i>
Noctuidae	<i>Aletia panarista</i> Fletcher	af	<i>Oryza</i>
	<i>Aletia umbriger</i> a Saalmüller	af	<i>Oryza</i>
	<i>Anomis luridula</i> Guenée	nt	<i>Gossypium</i>
	<i>Gnamptonyx innexa</i> Walker	af	<i>Oryza</i>
	<i>Hiccoda nigripalpis</i> Walker	or	<i>Oryza</i>
	<i>Leucania albistigma</i> Moore	or	<i>Oryza</i>
	<i>Leucania compta</i> Moore	or	<i>Oryza</i>
	<i>Leucania roseilinea</i> Walker	or	<i>Oryza</i>
	<i>Maliattha signifera</i> Walker	or	<i>Oryza</i>
	<i>Rhododactyla elicrina</i> Felder	af	<i>Oryza</i>
	<i>Rivula atimeta</i> Swinhoe	or	<i>Oryza</i>
	<i>Rivula continentalis</i> Gaede	af	<i>Oryza</i>
	<i>Rivula innotabilis</i> Swinhoe	or	<i>Oryza</i>
	<i>Sesamia venosata</i> Moore	or	<i>Oryza</i>
	<i>Spodoptera pulchella</i> Herrich-Schäffer	nt	<i>Gossypium</i>
	<i>Trichoplusia indicator</i> Walker	af	<i>Oryza</i>
Nymphalidae	<i>Bicyclus dorothea</i> Cramer	af	<i>Oryza</i>
	<i>Bicyclus vulgaris</i> Butler	af	<i>Oryza</i>
	<i>Mycalesis mamerta</i> Stoll	or	<i>Oryza</i>

Table 3. Continued.

	<i>Mycalesis nr. lorna</i> Grose-Smith	au	<i>Oryza</i>
	<i>Mycalesis visala</i> Moore	or	<i>Oryza</i>
Pieridae	<i>Zegris eupheme</i> Esper	pl	<i>Hirschfeldia</i>
Pyralidae	<i>Adelpherupa flavescens</i> Hampson	af	<i>Oryza</i>
	<i>Ancylolomia japonica</i> Zeller	ow	<i>Oryza</i>
	<i>Ancylosis convexella</i> Lederer	af	<i>Oryza</i>
	<i>Bleszynskia malacelloides</i> Bleszynski	or	<i>Oryza</i>
	<i>Catagela adjurella</i> Walker	or	<i>Oryza</i>
	<i>Chilo aleniella</i> Strand	af	<i>Oryza</i>
	<i>Chilo nr. partellus</i> Swinhoe	or	<i>Oryza</i>
	<i>Cnaphalocrocis bilinealis</i> Hampson	or	<i>Oryza</i>
	<i>Endotricha melanobasis</i> Hampson	or	<i>Oryza</i>
	<i>Epina dichromella</i> Walker	or	<i>Oryza</i>
	<i>Mabra eryxalis</i> Walker	or	<i>Oryza</i>
	<i>Marasmia ruralis</i> Walker	or	<i>Oryza</i>
	<i>Metoeca foedalis</i> Guenée	or	<i>Oryza</i>
	<i>Panalipa immeritalis</i> Walsingham	or	<i>Oryza</i>
	<i>Parerupa africana</i> Aurivillius	af	<i>Oryza</i>
	<i>Scirpophaga gilviberbis</i> Zeller	af; or	<i>Oryza</i>
	<i>Scirpophaga melanoclista</i> Meyrick	af	<i>Oryza</i>
	<i>Scirpophaga subumbrosa</i> Meyrick	af	<i>Oryza</i>
	<i>Zovax vangoghi</i> Bleszynski	af	<i>Oryza</i>
Thyrididae	<i>Opula spilotata</i> Warren	af	<i>Oryza</i>

¹ Species feeding only on a *Bt* manipulated plant genus but with a distribution outside the original distribution of the crop species and its close allies/progenitors are excluded on the grounds that they must have alternative hosts. Data from The Natural History Museum's HOSTS database (see Robinson, 1999). Distribution is indicated by a two-letter code, thus: af = Afrotropical region; au = Australasia; na = Nearctic region; nt = Neotropical region; or = Oriental region; ow = Old World; pl = Palearctic region.

species: *Actebia fennica*, *Agrotis ipsilon*, *Chilo suppressalis*, *Elasmopalpus lignosellus*, *Heliocoverpa zea*, *H. armigera*, *Heliothis virescens*, *Manduca sexta*, *Mamestra brassicae*, *Mamestra configurata*, *Pieris rapae*, *Plutella xylostella*, *Plodia interpunctella*, *Spodoptera frugiperda*, and *Trichoplusia ni*. Susceptibility levels for most non-target species are not available, either because no tests have been conducted or because test data on proprietary (especially genetically modified) proteins are confidential business information (Letourneau et al., 2002; van Frankenhuyzen and Nystrom, 1999).

Even limited data on the susceptibility of target pests to *Bt* crop toxins could be helpful if the pests represent a range of lepidopteran families, and if extrapolation to

non-target species in the same taxonomic group is reasonably accurate. The available data on susceptibility levels among species, however, suggest that these traits do not fall cleanly along broad taxonomic lines, such as suborders or families or even genera. For the lepidopteran pests examined, variability in susceptibility exists among closely related taxa, among different instars (or sizes) of the same species, and depends upon the particular protein being expressed by the plant, transgenic event, and the crop line, which can determine both the level of Cry protein expression and what plant tissues express the trait (Acciarri et al., 2000; Archer et al., 2000; Ashfaq et al., 2000; Macintosh et al., 1990; van Frankenhuyzen et al., 1991).

Table 4. Number of Lepidoptera species feeding on the indicated hostplant or hostplants shows the pattern and frequency of shared hostplants in Brassicaceae (species listed in and abbreviated from Appendix 1) among 199 Lepidoptera species (subspecific taxa not differentiated); 126 species are recorded from a single hostplant from within this group.

# Lepidopteran species	<i>B. juncea</i>	<i>B. napus</i>	<i>B. nigra</i>	<i>B. oleracea</i>	<i>B. rapa</i>	<i>Cak. edentula</i>	<i>Cak. maritima</i>	<i>Car. californica</i>	<i>H. incana</i>	<i>R. raphanistrum</i>	<i>R. sativus</i>	<i>S. arvensis</i>
1												
2												
1												
1												
4												
1												
3												
4												
1												
7												
1												
1												
1												
1												
5												
4												
1												
3												
1												
1												
2												
1												
1												
1												
3												
2												
6												
1												
1												

Assessing environmental consequences of transgene escape

Table 4. Continued.

# Lepidopteran species	<i>B. juncea</i>	<i>B. napus</i>	<i>B. nigra</i>	<i>B. oleracea</i>	<i>B. rapa</i>	<i>Cak. edentula</i>	<i>Cak. maritima</i>	<i>Car. californica</i>	<i>H. incana</i>	<i>R. raphanistrum</i>	<i>R. sativus</i>	<i>S. arvensis</i>
13												
1												
7												
86												
2												
6												
1												
3												
3												
1												
9												
2												

Table 5. Number of Lepidoptera species feeding on the indicated hostplant or hostplants shows the pattern and frequency of shared hostplants in Poaceae (species listed in and abbreviated from Appendix 1) among 571 Lepidoptera species (subspecific taxa not differentiated); 472 species are recorded from a single hostplant from within this group.

# Lepidopteran species	<i>O. glaberrima</i>	<i>O. sativa</i>	<i>Z. mays</i>	<i>Z. mexicana</i>
278				
193				
96				
2				
1				
1				

Table 6. Number of Lepidoptera species feeding on the indicated hostplant or hostplants shows the pattern and frequency of shared hostplants in Malvaceae (*Gossypium*) (species listed in and abbreviated from Appendix 1) among 44 Lepidoptera species (subspecific taxa not differentiated); 34 species are recorded from a single hostplant from within this group.

# Lepidopteran species	<i>G. barbadense</i>	<i>G. hirsutum</i>	<i>G. tomentososa</i>
1			
12			
21			
9			
1			

According to available data, non-target lepidopterans also vary greatly in their susceptibility to *Bt* sprays (e.g. Johnson et al., 1995; Wagner et al., 1996). *Bt* sprays were toxic to cinnabar moth larvae *Tyria jacobaea* (L.) only when they were exposed to the toxins in later instars (James et al., 1993). Peacock et al. (1998) showed that 27 of 42 species of forest Lepidoptera tested suffered mortality from *Bt* var. *kurstaki* sprays, especially when treated as early instars. Both susceptible and non-susceptible larvae were found in most of the seven families tested (Papilionidae, Nymphalidae, Geometridae, Lasiocampidae, Saturniidae, and Noctuidae). For example, species were found in both Geometridae and Noctuidae whose larvae, when exposed to *Bt* sprays, had no mortality or experienced 100% mortality.

This variability in susceptibility may extend to the population level. As has been documented by Bourguet et al. (2000) for the European Corn Borer, if the population genetics of pest species is such that some isolation exists between individuals exploiting crop plants and those in the same species feeding on non-crop hosts, then extrapolation from the little we do know about pest susceptibility to *Bt* crops may be misleading. As a further complication in terms of predicting susceptibility levels of non-target Lepidoptera, we expect there to be interactions between effects of secondary plant compounds in the host plant and the results of exposure to *Bt* proteins (e.g. Navon, 1993; Krishik et al., 1988; discussed such interactions between plant compounds and *Bt* toxins in spray formulations). Some substances, such as L-canavanine and tannin, were shown to enhance the toxicity of *Bt* proteins (Felton and Dahlman, 1984; Schuster and Calderone, 1986). In other cases, the delivery of toxic protein *via* plant tissues will increase the mortality rate for herbivores compared to that experienced when anti-bacterial secondary compounds fed upon by the herbivore inhibit toxin production in the gut (Reichelderfer, 1991). Hedin et al. (1978) found that cotton extracts suppressed the growth of *B. thuringiensis*.

Inspired by the findings of Losey and colleagues (Losey et al., 1999, 2002) that monarch butterflies suffer mortality when larvae fed on event 176 *Bt* corn pollen, some susceptibility data for non-target lepidopterans to *Bt* toxins expressed in plant tissue are accumulating (Jesse and Obyrcki, 2000; Hellmich 2001; Sears et al., 2001; Zangerl et al., 2001). However, the susceptibility of most caterpillars that act as significant herbivores of *Bt* crops or the wild relatives of *Bt* crops remains unknown and substantially unpredictable.

Fitness and other effects of lepidopterans on wild plants

Lepidoptera are the primary defoliators in agroecosystems (Barbosa, 1993), and certainly damage marketable products in agriculture. But are caterpillars a good candidate for controlling populations of wild plants (Fig. 1, question 8)? Perhaps data from programs on biological control of weeds, where wild plant populations have indeed been regulated and maintained at low densities by herbivores, provide the strongest evidence that herbivores play a critical role in reducing wild plant fitness and invasiveness (e.g. Story et al., 2000; Volenberg et al., 1999). Of course, these herbivores are selected specifically to control plants, and include some "alien" introductions uncontrolled by an endemic enemy loading. So these may, in aggregate, effect greater levels of weed control than would be expected for the suite of lepidopterans that could be excluded from *Bt* crops and resistant wild relatives. However, selection criteria for herbivores for biological weed control agents could perhaps play a part in predicting which are the key herbivores of interest in risk assessment.

A rich body of knowledge is certainly developing as critical control points in the life cycle of weeds (e.g. juvenile survival, seed development, or overwinter survival) are identified as strong determining factors in the population dynamics of the plant (Doak, 1992; Parker, 2000; Shea and Kelly, 1998). In some weed species, seedlings and juveniles appear to be the most susceptible life stages. Individuals at these stages are relatively easy to kill, and significant reductions in their numbers will reduce the overall weed status of the plant (Kriticos et al., 1999). If, on the other hand, these same controls were already functioning in a natural population of wild plants, removal of the controlling factors through plant resistance would release the plant, resulting in higher population densities and/or changes in invasiveness. Therefore, researchers must pay attention to whether or not the lepidopteran herbivores affected by *Bt* based resistance are indeed those species that attack the plant at control points in the life cycle – if, indeed, control points in the wild species of interest are known.

Lepidopterans do meet one important criterion for host plant regulation; they can reduce plant fitness (e.g. Agrawal, 1999; Koptur, 1990; Maron, 1998; Marquis, 1992, 1984; Paulissen, 1987; Pilson, 2000; Strauss et al., 1999). Caterpillar defoliation, root damage or vascular tissue damage sometimes work in concert with other stress factors such as plant-plant competition or herbivory by other arthropods (James et al., 1993; Juenger and

Bergelson, 1998). Specific research on the effects of *Bt* based resistance in wild *Brassica* populations has demonstrated effects of herbivory on plant fitness, especially when other stresses, such as poor soil quality and interspecific plant competition, are present (Bergelson, 1994; Meyer, 2000). Stewart et al. (1997) showed that transgenic, insect-resistant *B. napus* showed lower levels of defoliation, decreased mortality, and higher seed output compared to non-transgenic plants when grown in cultivated plots. Snow et al. (2003) demonstrated strong fecundity benefits of a single *Bt* transgene conferring insect-resistance in wild sunflowers. Population level impacts of changes in individual plant fitness (such as increased invasiveness or range expansion) can be predicted using demographic models with data collected from small-scale field experiments (Caswell, 2001; Kareiva et al., 1996; Marvier and Kareiva, 1999; Snow et al., 2003).

Caterpillars can also have indirect effects on wild plants in their habitats that may be relevant to risk assessments. Feeding by caterpillars can induce plant resistance against other herbivores (Agrawal, 1999; Agrawal et al., 1999) and/or can increase specific volatiles, which act as attractants for parasitoids and predators of the herbivore in question (e.g. Geervliet et al., 1997; McCall et al., 1994; Turlings et al., 1998). Caterpillar feeding can even cause unpredicted, negative effects on other plant species of interest in the same habitat. For example, Callaway et al. (1999) showed how a biological control agent (knapweed root moth) introduced to reduce the invasiveness of a weed and encourage the growth of native species actually caused a reduction in the native plant's fitness *via* root exudate mediated effects triggered by the lepidopteran. Damage from caterpillars can also serve as a potential selective factor in the evolution of flowering phenology (Pilson, 2000), determine the level of fitness depression caused by unrelated insects (Juenger and Bergelson, 1998; Naber and Aarssen, 1998; Pilson, 1996), reduce pollinator visitation (Strauss et al., 1999), variably affect plant fitness depending upon the timing or pattern of damage (Marquis, 1992; Mauricio et al., 1993), and cause increased biodiversity in the endophagous herbivore community (Tschamtkke, 1999).

Clearly, many factors interact to determine the success of a novel plant at a given site and time of introduction, including abiotic factors and the abundance and identities of mutualists, competitors, herbivores, etc. (Crawley et al., 1996). As more traits are added to crop plants, risk assessment of the consequences of gene flow will be more complex. However, predicting the potential for weediness and invasiveness of plant species

in different habitats is extremely important given the fact that invasions can lead to a reduction in biological diversity and threaten ecosystem integrity (Daehler and Strong, 1996).

CONCLUSION

Hoffman (1990) used the incorporation of *Bt* endotoxins in crop plants as a case study for posing a series of initial questions about possible environmental consequences of transgenic crops. She speculated about plant community effects of increased survival, reproduction or invasiveness of wild crop relatives, the consequences of increased competitive ability on plant biodiversity, and long distance effects of susceptible pollinators whose populations have been reduced by toxic host plants. Over a decade later, we have a greater appreciation for the complexity of insect-plant and plant-plant interactions, but the available data for predicting environmental consequences of transgenic traits remain weak. Despite the expanded cultivation of *Bt* crops in the USA and worldwide, very basic ecological questions remain unanswered, creating a scientific vacuum instead of a scientific foundation for the assessment of environmental effects. The overwhelming conclusion of recent studies is that gene flow will occur if there are wild relatives in the region that can hybridize with the crop (Kareiva et al., 1994; Klinger and Ellstrand, 1994). In the absence of barriers to the incorporation and expression of the trait (and its promoters) over time and expansion of the acreage and distribution of *Bt* crops, *cry* genes will likely enter wild plant populations. Kareiva et al. (1994) urged that ecologists begin to fill information gaps about the consequences of such gene flow to wild gene pools in order to have the tools to make regulatory decisions and to mitigate harmful consequences. These information gaps include basic answers about the forces that control the distribution, abundance and diversity of wild plant species in terrestrial communities (e.g. Doak, 1991; Letourneau and Dyer, 1999; McNaughton, 1986; Price, 1992). Within this context, we need to understand the influence of *Bt*-based toxins on naturally occurring Lepidoptera (Smith and Couche, 1991), and the actual role of lepidopterans as regulating forces for plants in natural and agricultural habitats.

Theoretically, an herbivore resistance trait could indeed increase fitness of weeds in natural populations and its invasiveness in the community. Yet we are faced with scientific controversies about the role of consumer dynamics as forces controlling plant population levels and community structure. To predict the outcome of transgene escape, manipulative experiments become

necessary but are not available (Fretwell, 1977; Kareiva et al., 1994; Marvier and Kareiva, 1999; McNaughton, 1986; NRC, 2002; Royal Society of Canada, 2000; Strong, 1984, 1992; Turkington et al., 1993). To date, predictions about the behavior of non-target lepidopterans on wild crop relatives must be made in the absence of any comprehensive species list of these herbivores. If none of these species is susceptible to *Bt* based endotoxins, or none is currently regulating populations of their host plant, then increased weediness is not likely (Fig. 1). If susceptible non-target herbivores are not rare and endangered, relied upon as genetic stock in refugia against resistance development, acting as important pollinators in the ecosystem, nor fulfilling any other key function, then the environmental price for transgene transfer from commercialized *Bt* crops to their wild relatives may be insignificant. Unfortunately, the scientific basis for assessing the queries Hoffman (1990) posed over a decade ago remains inadequate, and the challenges for environmental researchers and regulators will only increase as they ponder biosafety issues for multiple, stacked traits in a wider range of plants, in a context of global trade. Attempts at greater transparency in the regulatory decision process will encourage a step-by-step framework for analysis, demonstrate strengths and weakness in the assessments, and aid in identifying critical research areas.

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Appendix 1

The Lepidoptera that feed on *Bt* modified cole crops, cotton, rice or their close relatives

¹ Hostplant specificity is indicated by number of plant families and genera recorded as the food plants of the species, thus "10/24" indicates that ten families and twenty-four genera of plants are recorded as hosts. Where the number of hostplant families exceeds that of the number of genera, excess families are each for a record in

which no plant genus is specified. ² Distribution is indicated by a two-letter code, thus: af = Afrotropical region; au = Australasia and Pacific; cm = cosmopolitan; hl = Holarctic region (Nearctic + Palearctic); hw = Hawaii; ia = Indo-Australian region (Oriental + Australasia); na = Nearctic region; nt = Neotropical region; nw = New World (Nearctic + Neotropical regions); nz = New Zealand; or = Oriental region; ow = Old World; pl = Palearctic region. Distribution is simplified from individual records and may involve overlap and/or duplication. Data from The Natural History Museum's HOSTS database.

BRASSICACEAE¹

Brassica juncea

Arctiidae: *Syntomis sperbius* Fabricius [3/4] (or). ²

Geometridae: *Hemithea costipunctata* Moore [7/10] (or).

Noctuidae: *Agrotis ipsilon* Hufnagel [30/74] (af; au; cm; hw; ia; na; nt; nz; or; ow; pl); *Chrysodeixis eriosoma* Doubleday [18/29] (au; ia; or; pl); *Spodoptera litura* Fabricius [69/166] (af; au; cm; ia; nt; or; ow); *Tiracola plagiata* Walker [30/54] (au; ia; or); *Trichoplusia ni brassicae* Riley [1/1] (or); *Trichoplusia orichalcea* Fabricius [24/57] (af; au; or; ow); *Zurobata vacillans* Walker [7/8] (au; or).

Pieridae: *Appias libythea* Fabricius [3/5] (or); *Artogeia canidia* Linnaeus [2/4] (or); *Ascia monuste monuste* Linnaeus [4/7] (nt); *Hesperocharis marchalii marchalii* Guérin-Méneville [3/4] (nt); *Phoebis statira* Cramer [2/2] (nt); *Pieris brassicae* Linnaeus [6/24] (cm; or; pl); *Pieris helice johnstoni* Crowley [2/3] (af); *Pieris rapae* Linnaeus [6/31] (au; cm; hw; na; nz; or; pl); *Pieris rapae crucivora* Boisduval [3/6] (or; ow); *Pontia helice* Linnaeus [3/9] (af).

Pyralidae: *Corcyra cephalonica* Stainton [19/39] (af; cm; hw; na; nt; or); *Crocidolomia pavonana* Fabricius [7/13] (af; au; cm; or; ow); *Diaphania indica* Saunders [9/19] (af; au; cm; or; pl); *Hellula undalis* Fabricius [4/11] (af; au; hw; ia; or; ow); *Omiodes diemenalis* Guenée [6/29] (au; ia; or).

Tortricidae: *Adoxophyes privatana* Walker [31/53] (ia; or; ow; pl).

Yponomeutidae: *Plutella xylostella* Linnaeus [11/22] (af; au; cm; hw; ia; na; nt; or; pl).

Brassica napus

Geometridae: *Xanthorhoe designata* Hufnagel [2/6] (na; pl); *Xanthorhoe fluctuata* Linnaeus [2/7] (pl).

Hepialidae: *Hepialus humuli* Linnaeus [12/19] (pl); *Korscheltellus lupulina* Linnaeus [10/18] (pl).

Noctuidae: *Autographa gamma* Linnaeus [25/75] (cm; na; nt; pl); *Discestra trifolii* Hufnagel [17/34] (cm; na; or; pl); *Euxoa messoria* Harris [16/27] (na); *Euxoa nigricans* Linnaeus [11/12] (hl; pl); *Lacinipolia renigera* Stephens [12/18] (na; pl); *Mamestra brassicae* Linnaeus [14/27] (or; pl); *Mamestra configurata* Walker [16/33] (na; nt); *Melanchra picta* Harris [26/48] (hl; na); *Pseudaletia unipuncta* Haworth [18/53] (au; cm; hw; na; nt; or; pl); *Spodoptera ornithogalli* Guenée [25/53] (cm; na; nt); *Trichoplusia ni* Hübner [27/65] (af; cm; hw; na; nt; or; pl); *Trichordestra legitima* Grote [11/22] (na).

Pieridae: *Anthocharis sara* Lucas [1/16] (na); *Ascia monuste eubotea* Godart [4/7] (nt); *Euchloe ausonides* Lucas [1/12] (na); *Pieris brassicae* Linnaeus [6/24] (cm; or; pl); *Pieris napi* Linnaeus [4/21] (hl; na; or; pl); *Pieris rapae* Linnaeus [6/31] (au; cm; hw; na; nz; or; pl); *Pieris rapae rapae* Linnaeus [4/14] (au; cm).

Pyralidae: *Hellula phidilealis* Walker [3/6] (cm; na; nt); *Hellula rogatalis* Hulst [2/5] (na).

Sphingidae: *Manduca sexta* Linnaeus [7/16] (na; nt; nw).

Yponomeutidae: *Plutella xylostella* Linnaeus [11/22] (af; au; cm; hw; ia; na; nt; or; pl).

Brassica nigra

Arctiidae: *Arachnis picta* Packard [8/13] (na); *Pericallia ricini* Fabricius [31/45] (or); *Spilosoma obliqua* Walker [27/54] (or).

Noctuidae: *Agnorisma badinodis* Grote [9/11] (na); *Agrotis ipsilon* Hufnagel [30/74] (af; au; cm; hw; ia; na; nt; nz; or; ow; pl); *Agrotis orthogonia* Morrison [11/27] (na); *Copablepharon viridisparva* Dod [1/2] (na); *Euxoa auxiliaris* Grote [16/42] (na); *Ochropleura flammata* Denis and Schiff. [13/19] (or; ow; pl); *Peridroma saucia* Hübner [40/86] (cm; na; nt; pl); *Spodoptera exigua* Hübner [35/83] (af; au; cm; hw; na; or; pl); *Spodoptera litura* Fabricius [69/166] (af; au; cm; ia; nt; or; ow); *Trichoplusia ni* Hübner [27/65] (af; cm; hw; na; nt; or; pl).

Pieridae: *Anthocharis sara* Lucas [1/16] (na); *Euchloe ausonides* Lucas [1/12] (na); *Pieris brassicae* Linnaeus [6/24] (cm; or; pl); *Pieris napi* Linnaeus [4/21] (hl; na; or; pl); *Pieris protodice* Boisduval and Le Co [1/2] (na); *Pieris rapae* Linnaeus [6/31] (au; cm; hw; na; nz; or; pl); *Pontia beckerii* Edwards [2/8] (na); *Pontia occidentalis* Reakirt [4/18] (na; pl); *Pontia protodice* Boisduval and LeC. [3/23] (na; nt).

Psychidae: *Apterona crenulella helix* Siebold [19/39] (pl).

Pyralidae: *Crociodomia pavonana* Fabricius [7/13] (af; au; cm; or; ow); *Eustixia pupula* Hübner [2/3] (na); *Hellula undalis* Fabricius [4/11] (af; au; hw; ia; or; ow); *Plodia interpunctella* Hübner [25/48] (af; cm; na; nt; or; pl).

Yponomeutidae: *Plutella xylostella* Linnaeus [11/22] (af; au; cm; hw; ia; na; nt; or; pl).

Brassica oleracea

Arctiidae: *Alpenus investigatorum* Karsch [15/24] (af; pl); *Amsacta lactinea* Cramer [26/45] (or); *Estigmene acrea* Drury [23/46] (na; nt; nw); *Hypercompe abdominalis* Walker [2/2] (nt); *Hypercompe indecisa* Walker [13/19] (nt); *Hypercompe scribonia* Stoll [15/17] (na); *Nyctemera baulus* Boisduval [3/4] (au; or); *Paracles fusca* Walker [13/20] (nt); *Pericallia ricini* Fabricius [31/45] (or); *Spilosoma obliqua* Walker [27/54] (or); *Spilosoma sumatrana* Swinhoe [11/15] (or); *Spilosoma virginica* Fabricius [44/86] (cm; na); *Teracotona submacula* Walker [4/5] (af).

Cosmopterigidae: *Pyroderces badia* Hodges [16/18] (hw; na).

Geometridae: *Eupithecia pulchellata* Stephens [2/2] (pl); *Hemithea costipunctata* Moore [7/10] (or); *Scopula fibulata* Guenée [6/7] (or); *Xanthorhoe designata* Hufnagel [2/6] (na; pl); *Xanthorhoe iduata* Guenée [2/2] (na); *Xanthorhoe saturata* Guenée [4/5] (or; pl).

Limacodidae: *Parasa lepida* Cramer [35/77] (ia; or; ow).

Lymantriidae: *Clethrogyna turbata* Butler [20/35] (or); *Olene mendosa* Hübner [50/97] (af; au; ia; or); *Somena scintillans* Walker [38/76] (or).

Noctuidae: *Abagrotis alternata* Grote [8/12] (na);

Agrotis gladiaria Morrison [11/17] (na); *Agrotis infusa* Boisduval [7/9] (au); *Agrotis ipsilon* Hufnagel [30/74] (af; au; cm; hw; ia; na; nt; nz; or; ow; pl); *Agrotis malefida* Guenée [11/19] (na; nt; nw); *Agrotis repleta* Walker [11/20] (nt); *Agrotis segetum* Denis and Schiff. [21/45] (af; or; ow; pl); *Agrotis subterranea* Fabricius [17/39] (na; nt; nw); *Agrotis vetusta* Walker [13/20] (na); *Anagrapha falcifera* Kirby [11/17] (na); *Apamea amputatrix* Fitch [7/9] (na); *Apamea devastator* Brace [9/19] (na); *Argyrogramma signata* Fabricius [7/12] (af; au; or; ow); *Autographa californica* Speyer [26/44] (na); *Autographa gamma* Linnaeus [25/75] (cm; na; nt; pl); *Autographa precatationis* Guenée [11/17] (na); *Chrysodeixis acuta* Walker [18/26] (af; or; ow); *Chrysodeixis chalcites* Esper [28/75] (af; au; cm; or; ow; pl); *Chrysodeixis eriosoma* Doubleday [18/29] (au; ia; or; pl); *Condica sutor* Guenée [3/11] (af; na; nt); *Discestra trifolii* Hufnagel [17/34] (cm; na; or; pl); *Ercheia cyllaria* Cramer [5/4] (or); *Euxoa auxiliaris* Grote [16/42] (na); *Euxoa infausta* Walker [4/6] (na); *Euxoa intrita* Morrison [2/2] (na); *Euxoa messoria* Harris [16/27] (na); *Euxoa ochrogaster* Guenée [10/18] (na; pl); *Euxoa scandens* Riley [9/14] (na); *Euxoa tessellata* Harris [15/28] (na); *Feltia jaculifera* Guenée [16/30] (na); *Feltia subgothica* Haworth [9/18] (cm; na; nw; pl); *Helicoverpa armigera* Hübner [40/102] (af; au; cm; ia; na; nt; nz; or; ow; pl); *Helicoverpa zea* Boddie [38/111] (af; hw; na; nt; nw; or); *Lacanobia subjuncta* Grote and Robinson [12/14] (na); *Lacinipolia renigera* Stephens [12/18] (na; pl); *Litoprosopus futilis* Grote and Robinson [2/3] (na); *Lycophotia porphyrea* Denis and Schiff. [7/12] (hw; pl); *Mamestra brassicae* Linnaeus [14/27] (or; pl); *Mamestra configurata* Walker [16/33] (na; nt); *Mamestra curialis* Smith [8/8] (na); *Megalographa biloba* Stephens [15/22] (na; nw; pl); *Melanchra picta* Harris [26/48] (hl; na); *Noctua pronuba* Linnaeus [15/22] (hl; na; or; pl); *Papaipema nebris* Guenée [31/86] (na); *Peridroma saucia* Hübner [40/86] (cm; na; nt; pl); *Pseudaletia unipuncta* Haworth [18/53] (au; cm; hw; na; nt; or; pl); *Pseudoleucania bilitura* Guenée [3/4] (nt); *Pseudoplusia includens* Walker [22/46] (na; nt); *Rachiplusia nu* Guenée [9/18] (nt); *Spaelotis clandestina* Harris [18/25] (na); *Spodoptera dolichos* Fabricius [14/22] (na; nt); *Spodoptera eridania* Stoll [31/63] (na; nt; nw); *Spodoptera exigua* Hübner [35/83] (af; au; cm; hw; na; or; pl); *Spodoptera frugiperda* Smith [34/91] (af; cm; na;

nt; nw); *Spodoptera littoralis* Boisduval [25/43] (af; na; or; ow; pl); *Spodoptera litura* Fabricius [69/166] (af; au; cm; ia; nt; or; ow); *Spodoptera ornithogalli* Guenée [25/53] (cm; na; nt); *Sunira bicolorago* Guenée [8/9] (na); *Syngrapha circumflexa* Linnaeus [7/8] (af; or; pl); *Tiracola plagiata* Walker [30/54] (au; ia; or); *Trichoplusia ni* Hübner [27/65] (af; cm; hw; na; nt; or; pl); *Trichoplusia ni brassicae* Riley [1/1] (or); *Trichoplusia orichalcea* Fabricius [24/57] (af; au; or; ow); *Trichordestra legitima* Grote [11/22] (na); *Xestia c-nigrum* Linnaeus [31/51] (hl; na; or; pl); *Xylena vetusta* Hübner [13/21] (na; pl).

Nymphalidae: *Amauris tartarea* Mabilie [1/1] (af).

Pieridae: *Appias libythea* Fabricius [3/5] (or); *Appias libythea peducea* Fruhstorfer [2/2] (or); *Artogeia canidia* Linnaeus [2/4] (or); *Ascia monuste* Linnaeus [5/14] (na; nt; nw); *Ascia monuste automate* Burmeister [1/1] (nt); *Ascia monuste eubotea* Godart [4/7] (nt); *Ascia monuste monuste* Linnaeus [4/7] (nt); *Hebomoia glaucippe* Linnaeus [2/5] (or); *Hesperocharis marchalii* Guérin-Méneville [3/4] (nt); *Phoebis statira* Cramer [2/2] (nt); *Pieris brassicae* Linnaeus [6/24] (cm; or; pl); *Pieris canidia* Sparrman [4/10] (or); *Pieris napi* Linnaeus [4/21] (hl; na; or; pl); *Pieris pylotis* Godart [2/3] (nt); *Pieris rapae* Linnaeus [6/31] (au; cm; hw; na; nz; or; pl); *Pieris rapae crucivora* Boisduval [3/6] (or; ow); *Pieris rapae rapae* Linnaeus [4/14] (au; cm); *Pontia protodice* Boisduval and LeC. [3/23] (na; nt); *Tatochila autodice* Hübner [4/9] (nt).

Psychidae: *Apterona crenulella helix* Siebold [19/39] (pl).

Pyralidae: *Chilo suppressalis* Walker [3/19] (af; au; hw; ia; na; or; ow); *Crocidolomia pavonana* Fabricius [7/13] (af; au; cm; or; ow); *Eustixia pupula* Hübner [2/3] (na); *Evergestis rimosalis* Guenée [1/2] (cm; na; nt); *Hellula phidilealis* Walker [3/6] (cm; na; nt); *Hellula rogatalis* Hulst [2/5] (na); *Hellula undalis* Fabricius [4/11] (af; au; hw; ia; or; ow); *Herpetogramma submarginalis* Swinhoe [6/9] (au; or); *Loxostege sticticalis* Linnaeus [17/35] (hl; na; pl); *Plodia interpunctella* Hübner [25/48] (af; cm; na; nt; or; pl); *Udea ferrugalis* Hübner [9/16] (af; or; pl); *Udea rubigalis* Guenée [16/28] (na; nt; nw).

Sphingidae: *Hyles lineata* Fabricius [36/61] (af; au; na; nt; nw; pl).

- Tineidae:** *Trachycentra calamias* Meyrick [4/4] (au).
- Tortricidae:** *Amorbia emigratella* Busck [22/30] (hw; na; nt); *Cnephasia asseclana* Denis and Schiff. [9/15] (na; pl); *Selania leplastriana* Curtis [1/5] (pl).
- Yponomeutidae:** *Leuroperna sera* Meyrick [1/1] (au; or; ow); *Plutella xylostella* Linnaeus [11/22] (af; au; cm; hw; ia; na; nt; or; pl).
- Brassica oleracea acephala**
- Pieridae:** *Ascia monuste* Linnaeus [5/14] (na; nt; nw); *Ascia monuste monuste* Linnaeus [4/7] (nt); *Pieris rapae* Linnaeus [6/31] (au; cm; hw; na; nz; or; pl).
- Sphingidae:** *Hyles lineata* Fabricius [36/61] (af; au; na; nt; nw; pl).
- Yponomeutidae:** *Plutella xylostella* Linnaeus [11/22] (af; au; cm; hw; ia; na; nt; or; pl).
- Brassica oleracea botrytis**
- Geometridae:** *Xanthorhoe fluctuata* Linnaeus [2/7] (pl).
- Lymantriidae:** *Euproctis varians* Walker [9/17] (or); *Sphrageidus virguncula* Walker [12/25] (or).
- Noctuidae:** *Aegoceropsis rectilinea* Boisduval [7/9] (af); *Melanchra picta* Harris [26/48] (hl; na); *Spodoptera litura* Fabricius [69/166] (af; au; cm; ia; nt; or; ow); *Trichoplusia orichalcea* Fabricius [24/57] (af; au; or; ow).
- Pieridae:** *Ascia monuste* Linnaeus [5/14] (na; nt; nw); *Pieris brassicae* Linnaeus [6/24] (cm; or; pl); *Pieris rapae* Linnaeus [6/31] (au; cm; hw; na; nz; or; pl); *Pieris rapae crucivora* Boisduval [3/6] (or; ow); *Pieris rapae rapae* Linnaeus [4/14] (au; cm); *Pontia protodice* Boisduval and LeC. [3/23] (na; nt).
- Pyralidae:** *Crocidolomia pavonana* Fabricius [7/13] (af; au; cm; or; ow).
- Tortricidae:** *Clepsis spectrana* Treitschke [22/32] (na; pl); *Selania leplastriana* Curtis [1/5] (pl).
- Yponomeutidae:** *Plutella xylostella* Linnaeus [11/22] (af; au; cm; hw; ia; na; nt; or; pl).
- Brassica oleracea bullata**
- Noctuidae:** *Agrotis segetum* Denis and Schiff. [21/45] (af; or; ow; pl); *Argyrogramma signata* Fabricius [7/12] (af; au; or; ow); *Spodoptera litura* Fabricius [69/166] (af; au; cm; ia; nt; or; ow); *Syngrapha circumflexa* Linnaeus [7/8] (af; or; pl).
- Pyralidae:** *Crocidolomia pavonana* Fabricius [7/13] (af; au; cm; or; ow); *Hellula undalis* Fabricius [4/11] (af; au; hw; ia; or; ow).
- Yponomeutidae:** *Plutella xylostella* Linnaeus [11/22] (af; au; cm; hw; ia; na; nt; or; pl).
- Brassica oleracea capitata**
- Arctiidae:** *Estigmene acrea* Drury [23/46] (na; nt; nw); *Spilosoma lubricipeda* Linnaeus [15/20] (or; pl); *Teracotona submacula* Walker [4/5] (af).
- Gelechiidae:** *Dichomeris oceanis* Meyrick [3/5] (pl).
- Geometridae:** *Scopula fibulata* Guenée [6/7] (or).
- Lasiocampidae:** *Chondrostega tingitana* Powell [3/3] (pl).
- Lymantriidae:** *Euproctis varians* Walker [9/17] (or); *Sphrageidus virguncula* Walker [12/25] (or).
- Noctuidae:** *Agrotis clavis* Hufnagel [5/6] (or; pl); *Agrotis ipsilon* Hufnagel [30/74] (af; au; cm; hw; ia; na; nt; nz; or; ow; pl); *Agrotis repleta* Walker [11/20] (nt); *Agrotis subterranea* Fabricius [17/39] (na; nt; nw); *Argyrogramma verruca* Fabricius [13/17] (na; nt; nw); *Autographa gamma* Linnaeus [25/75] (cm; na; nt; pl); *Autographa nigrisigna* Walker [7/13] (or; ow); *Chrysodeixis eriosoma* Doubleday [18/29] (au; ia; or; pl); *Cornutiplusia circumflexa* Linnaeus [5/5] (pl); *Discestra trifolii* Hufnagel [17/34] (cm; na; or; pl); *Euxoa messoria* Harris [16/27] (na); *Euxoa nigricans* Linnaeus [11/12] (hl; pl); *Euxoa ochrogaster* Guenée [10/18] (na; pl); *Euxoa tritici* Linnaeus [8/13] (pl); *Helicoverpa armigera* Hübner [40/102] (af; au; cm; ia; na; nt; nz; or; ow; pl); *Lacanobia nevadae* Grote [6/6] (na); *Lacanobia oleracea* Linnaeus [22/41] (pl); *Lacanobia pisi* Linnaeus [7/11] (pl); *Mamestra brassicae* Linnaeus [14/27] (or; pl); *Melanchra picta* Harris [26/48] (hl; na); *Mocis latipes* Guenée [10/37] (na; nt; nw); *Naenia typica* Linnaeus [15/24] (or; pl); *Nephelodes minians* Guenée [7/12] (na); *Noctua pronuba* Linnaeus [15/22] (hl; na; or; pl); *Peridroma saucia* Hübner [40/86] (cm; na; nt; pl); *Phlogophora meticulosa* Linnaeus [12/23] (pl); *Pseudoplusia includens* Walker [22/46] (na; nt); *Spodoptera eridania* Stoll [31/63] (na; nt; nw); *Spodoptera litura* Fabricius [69/166] (af; au; cm;

ia; nt; or; ow); *Trichoplusia ni* Hübner [27/65] (af; cm; hw; na; nt; or; pl); *Trichoplusia orichalcea* Fabricius [24/57] (af; au; or; ow); *Xestia c-nigrum* Linnaeus [31/51] (hl; na; or; pl).

Papilionidae: *Papilio polyxenes* Fabricius [5/29] (na; nt; nw).

Pieridae: *Appias drusilla* Cramer [3/4] (na; nt); *Ascia monuste* Linnaeus [5/14] (na; nt; nw); *Ascia monuste monuste* Linnaeus [4/7] (nt); *Leptophobia aripa* Boisduval [2/2] (nt); *Pieris brassicae* Linnaeus [6/24] (cm; or; pl); *Pieris canidia canidia* Sparrman [3/6] (or); *Pieris daplidice* Linnaeus [2/9] (af; or; ow; pl); *Pieris daplidice albidice* Oberthür [1/1] (pl); *Pieris napi* Linnaeus [4/21] (hl; na; or; pl); *Pieris rapae* Linnaeus [6/31] (au; cm; hw; na; nz; or; pl); *Pieris rapae crucivora* Boisduval [3/6] (or; ow); *Pieris rapae rapae* Linnaeus [4/14] (au; cm); *Pontia protodice* Boisduval and LeC. [3/23] (na; nt); *Tatochila autodice* Hübner [4/9] (nt).

Pyralidae: *Crociodolomia pavonana* Fabricius [7/13] (af; au; cm; or; ow); *Hellula hydralis* Guenée [1/1] (au); *Hellula phidilealis* Walker [3/6] (cm; na; nt); *Hellula undalis* Fabricius [4/11] (af; au; hw; ia; or; ow); *Herpetogramma submarginalis* Swinhoe [6/9] (au; or).

Tortricidae: *Selania leplastriana* Curtis [1/5] (pl).

Yponomeutidae: *Plutella xylostella* Linnaeus [11/22] (af; au; cm; hw; ia; na; nt; or; pl).

Brassica oleracea gemmifera

Noctuidae: *Mamestra brassicae* Linnaeus [14/27] (or; pl).

Pieridae: *Pieris brassicae* Linnaeus [6/24] (cm; or; pl); *Pieris napi* Linnaeus [4/21] (hl; na; or; pl); *Pieris rapae* Linnaeus [6/31] (au; cm; hw; na; nz; or; pl); *Pieris rapae rapae* Linnaeus [4/14] (au; cm).

Pyralidae: *Evergestis forficalis* Linnaeus [2/4] (ow; pl).

Tortricidae: *Clepsis spectrana* Treitschke [22/32] (na; pl).

Yponomeutidae: *Plutella xylostella* Linnaeus [11/22] (af; au; cm; hw; ia; na; nt; or; pl).

Brassica oleracea gongyloides

Noctuidae: *Spodoptera litura* Fabricius [69/166] (af; au; cm; ia; nt; or; ow).

Pieridae: *Pieris brassicae* Linnaeus [6/24] (cm; or; pl).

Brassica oleracea italica

Gelechiidae: *Phthorimaea operculella* Zeller [6/14] (af; au; cm; hw; na; nt; nw; or; ow; pl).

Noctuidae: *Agrotis ipsilon* Hufnagel [30/74] (af; au; cm; hw; ia; na; nt; nz; or; ow; pl).

Pieridae: *Pieris rapae rapae* Linnaeus [4/14] (au; cm).

Yponomeutidae: *Plutella xylostella* Linnaeus [11/22] (af; au; cm; hw; ia; na; nt; or; pl).

Brassica rapa

Arctiidae: *Spilosoma obliqua* Walker [27/54] (or); *Spilosoma virginica* Fabricius [44/86] (cm; na).

Geometridae: *Anacamptodes fragilaria* Grossbeck [15/24] (na).

Noctuidae: *Achaea janata* Linnaeus [33/74] (af; au; hw; ia; or); *Agrotis ipsilon* Hufnagel [30/74] (af; au; cm; hw; ia; na; nt; nz; or; ow; pl); *Agrotis segetum* Denis and Schiff. [21/45] (af; or; ow; pl); *Agrotis subterranea* Fabricius [17/39] (na; nt; nw); *Agrotis vetusta* Walker [13/20] (na); *Autographa californica* Speyer [26/44] (na); *Autographa gamma* Linnaeus [25/75] (cm; na; nt; pl); *Discestra trifolii* Hufnagel [17/34] (cm; na; or; pl); *Euxoa auxiliaris* Grote [16/42] (na); *Euxoa messoria* Harris [16/27] (na); *Feltia jaculifera* Guenée [16/30] (na); *Lacanobia oleracea* Linnaeus [22/41] (pl); *Lacanobia suasa* Denis and Schiff. [15/25] (pl); *Lacinipolia renigera* Stephens [12/18] (na; pl); *Mamestra brassicae* Linnaeus [14/27] (or; pl); *Mamestra configurata* Walker [16/33] (na; nt); *Melanchra picta* Harris [26/48] (hl; na); *Mocis latipes* Guenée [10/37] (na; nt; nw); *Noctua pronuba* Linnaeus [15/22] (hl; na; or; pl); *Peridroma saucia* Hübner [40/86] (cm; na; nt; pl); *Spodoptera dolichos* Fabricius [14/22] (na; nt); *Spodoptera frugiperda* Smith [34/91] (af; cm; na; nt; nw); *Spodoptera litura* Fabricius [69/166] (af; au; cm; ia; nt; or; ow); *Spodoptera ornithogalli* Guenée [25/53] (cm; na; nt); *Trichoplusia ni* Hübner [27/65] (af; cm; hw; na; nt; or; pl); *Trichordestra legitima* Grote [11/22] (na); *Tripseuxoa strigata* Hampson [4/7] (nt); *Xestia c-nigrum* Linnaeus [31/51] (hl; na; or; pl).

Pieridae: *Anthocharis sara* Lucas [1/16] (na); *Ascia monuste* Linnaeus [5/14] (na; nt; nw); *Ascia*

monuste monuste Linnaeus [4/7] (nt); *Belenois zochalia* Boisduval [3/8] (af); *Euchloe ausonides* Lucas [1/12] (na); *Hesperocharis marchalii marchalii* Guérin-Méneville [3/4] (nt); *Pieris brassicae* Linnaeus [6/24] (cm; or; pl); *Pieris napi* Linnaeus [4/21] (hl; na; or; pl); *Pieris rapae* Linnaeus [6/31] (au; cm; hw; na; nz; or; pl); *Pieris rapae rapae* Linnaeus [4/14] (au; cm); *Pontia protodice* Boisduval and LeC. [3/23] (na; nt); *Tatochila autodice* Hübner [4/9] (nt).

Psychidae: *Apterona crenulella helix* Siebold [19/39] (pl).

Pyralidae: *Corcyra cephalonica* Stainton [19/39] (af; cm; hw; na; nt; or); *Crocidolomia pavonana* Fabricius [7/13] (af; au; cm; or; ow); *Elasmopalpus lignosellus* Zeller [23/38] (cm; na; nt; nw); *Evergestis pallidata* Hufnagel [1/5] (hl; na; pl); *Hellula phidilealis* Walker [3/6] (cm; na; nt); *Hellula undalis* Fabricius [4/11] (af; au; hw; ia; or; ow); *Ostrinia nubilalis* Hübner [16/39] (au; cm; hl; na; or; pl).

Sphingidae: *Hyles lineata* Fabricius [36/61] (af; au; na; nt; nw; pl).

Yponomeutidae: *Leuoperna sera* Meyrick [1/1] (au; or; ow); *Plutella xylostella* Linnaeus [11/22] (af; au; cm; hw; ia; na; nt; or; pl).

Cakile edentula

Noctuidae: *Euxoa detersa* Walker [8/14] (na).

Pieridae: *Ascia monuste* Linnaeus [5/14] (na; nt; nw); *Pieris rapae* Linnaeus [6/31] (au; cm; hw; na; nz; or; pl); *Pontia protodice* Boisduval and LeC. [3/23] (na; nt).

Cakile maritima

Arctiidae: *Platyprepia virginalis* Boisduval [5/6] (na).

Noctuidae: *Agrotis ripae* Hübner [2/3] (pl); *Euxoa cursoria* Hufnagel [8/9] (na; pl); *Trichoplusia ni* Hübner [27/65] (af; cm; hw; na; nt; or; pl).

Pieridae: *Ascia monuste* Linnaeus [5/14] (na; nt; nw); *Pieris brassicae* Linnaeus [6/24] (cm; or; pl); *Pieris daplidice* Linnaeus [2/9] (af; or; ow; pl).

Cardamine californica

Pieridae: *Anthocharis sara* Lucas [1/16] (na); *Pieris napi* Linnaeus [4/21] (hl; na; or; pl).

Hirschfeldia incana

Arctiidae: *Arachnis picta* Packard [8/13] (na); *Arachnis picta picta* Packard [3/3] (na); *Notarctia proxima* Guérin-Méneville [8/9] (na); *Spilosoma vestalis* Packard [8/10] (na).

Pieridae: *Anthocharis sara* Lucas [1/16] (na); *Euchloe ausonides* Lucas [1/12] (na); *Pieris protodice* Boisduval and Le Co [1/2] (na); *Pieris rapae* Linnaeus [6/31] (au; cm; hw; na; nz; or; pl); *Pieris rapae rapae* Linnaeus [4/14] (au; cm); *Pontia protodice* Boisduval and LeC. [3/23] (na; nt); *Zegris eupheme* Esper [1/1] (pl).

Raphanus raphanistrum

Geometridae: *Xanthorhoe fluctuata* Linnaeus [2/7] (pl).

Noctuidae: *Autographa gamma* Linnaeus [25/75] (cm; na; nt; pl).

Pieridae: *Ascia monuste monuste* Linnaeus [4/7] (nt); *Pieris napi* Linnaeus [4/21] (hl; na; or; pl); *Pieris rapae* Linnaeus [6/31] (au; cm; hw; na; nz; or; pl); *Pieris rapae rapae* Linnaeus [4/14] (au; cm); *Tatochila autodice* Hübner [4/9] (nt).

Psychidae: *Apterona crenulella helix* Siebold [19/39] (pl).

Tortricidae: *Tortrix capensana* Walker [8/10] (af).

Raphanus sativus

Arctiidae: *Ocnogyna loewii* Zeller [4/4] (pl); *Spilosoma virginica* Fabricius [44/86] (cm; na).

Geometridae: *Xanthorhoe designata* Hufnagel [2/6] (na; pl).

Hepialidae: *Endoclita excrescens* Butler [3/4] (ow; pl).

Noctuidae: *Achaea janata* Linnaeus [33/74] (af; au; hw; ia; or); *Agrotis ipsilon* Hufnagel [30/74] (af; au; cm; hw; ia; na; nt; nz; or; ow; pl); *Agrotis longidentifera* Hampson [7/9] (af); *Apamea devastator* Brace [9/19] (na); *Brithysana speyeri* Felder and Rogenh. [9/12] (af); *Chrysodeixis eriosoma* Doubleday [18/29] (au; ia; or; pl); *Crassivesica bochus* Morrison [2/2] (na); *Discestra trifolii* Hufnagel [17/34] (cm; na; or; pl); *Euxoa auxiliaris* Grote [16/42] (na); *Euxoa messoria* Harris [16/27] (na); *Euxoa ochrogaster* Guenée [10/18] (na; pl); *Euxoa scandens* Riley [9/14] (na); *Euxoa tessellata* Harris [15/28] (na); *Hydraecia*

micacea Esper [15/27] (hl; na; pl); *Mamestra brassicae* Linnaeus [14/27] (or; pl); *Melanchra picta* Harris [26/48] (hl; na); *Peridroma saucia* Hübner [40/86] (cm; na; nt; pl); *Pseudaletia unipuncta* Haworth [18/53] (au; cm; hw; na; nt; or; pl); *Rachiplusia nu* Guenée [9/18] (nt); *Spodoptera exigua* Hübner [35/83] (af; au; cm; hw; na; or; pl); *Spodoptera litura* Fabricius [69/166] (af; au; cm; ia; nt; or; ow); *Spodoptera pecten* Guenée [7/15] (ia; or); *Trichoplusia ni* Hübner [27/65] (af; cm; hw; na; nt; or; pl); *Trichoplusia orichalcea* Fabricius [24/57] (af; au; or; ow).

Nymphalidae: *Vanessa cardui* Linnaeus [25/104] (af; au; cm; hw; na; or; pl).

Pieridae: *Anthocharis sara* Lucas [1/16] (na); *Artogeia canidia* Linnaeus [2/4] (or); *Ascia monuste* Linnaeus [5/14] (na; nt; nw); *Euchloe ausonides* Lucas [1/12] (na); *Pieris brassicae* Linnaeus [6/24] (cm; or; pl); *Pieris daplidice* Linnaeus [2/9] (af; or; ow; pl); *Pieris napi* Linnaeus [4/21] (hl; na; or; pl); *Pieris rapae* Linnaeus [6/31] (au; cm; hw; na; nz; or; pl); *Pieris rapae crucivora* Boisduval [3/6] (or; ow); *Pieris rapae rapae* Linnaeus [4/14] (au; cm); *Pontia protodice* Boisduval and LeC. [3/23] (na; nt); *Tatochila autodice* Hübner [4/9] (nt).

Pyralidae: *Achyra rantalis* Guenée [8/14] (na; nt; nw); *Crocidolomia pavonana* Fabricius [7/13] (af; au; cm; or; ow); *Evergestis forficalis* Linnaeus [2/4] (ow; pl); *Evergestis pallidata* Hufnagel [1/5] (hl; na; pl); *Hellula phidilealis* Walker [3/6] (cm; na; nt); *Hellula rogatalis* Hulst [2/5] (na); *Hellula undalis* Fabricius [4/11] (af; au; hw; ia; or; ow); *Udea rubigalis* Guenée [16/28] (na; nt; nw).

Sphingidae: *Manduca sexta* Linnaeus [7/16] (na; nt; nw).

Yponomeutidae: *Plutella xylostella* Linnaeus [11/22] (af; au; cm; hw; ia; na; nt; or; pl).

Sinapis arvensis

Noctuidae: *Spodoptera praefica* Grote [16/35] (na).

Pieridae: *Anthocharis sara* Lucas [1/16] (na); *Anthocharis sara sara* Lucas [1/7] (na); *Euchloe ausonides* Lucas [1/12] (na); *Pieris rapae* Linnaeus [6/31] (au; cm; hw; na; nz; or; pl); *Pontia protodice* Boisduval and LeC. [3/23] (na; nt).

Pyralidae: *Nomophila nearctica* Munroe [7/12] (na).

GRAMINEAE

Oryza glaberrima

Pyralidae: *Maliarpha separatella* Ragonot [1/2] (af; ow).

Tortricidae: *Dudua aprobola* Meyrick [20/37] (af; au; ia; or).

Oryza sativa

Arctiidae: *Alpenus maculosa* Stoll [14/24] (af); *Amata fortunei* de l'Orza [2/2] (or); *Amata huebneri* Boisduval [1/1] (or); *Amsacta lactinea* Cramer [26/45] (or); *Amsacta lineola* Fabricius [8/15] (or); *Asura calamaria* Moore [3/3] (or); *Cretonotos gangis* Linnaeus [8/19] (au; or); *Cretonotos leucanioides* Holland [4/4] (af; nt); *Cretonotos punctivitta* Walker [1/1] (af); *Estigmene senegalensis* Rothschild [1/1] (af); *Micralarctia punctulata* Wallengren [3/3] (af); *Paracles laboulbeni* Bar [1/1] (nt); *Schistophleps bipuncta* Hampson [1/1] (or); *Spilosoma nigricosta* Holland [1/2] (af); *Spilosoma scortilla* Wallengren [1/1] (af); *Thumatha fuscescens* Walker [1/1] (or).

Cossidae: *Phragmataecia purpureus* Fletcher [1/4] (or).

Eupterotidae: *Eupterote minor* Moore [2/2] (or); *Nisaga simplex* Walker [1/2] (or).

Gelechiidae: *Athrips studiosa* Meyrick [1/1] (or); *Helcystogramma arotraea* Meyrick [1/4] (or); *Helcystogramma nr. malacogramma* Meyrick [1/1] (af); *Pityocon xeropis* Meyrick [1/1] (or); *Sitotroga cerealella* Olivier [2/8] (af; cm; hw; na; nt; or).

Geometridae: *Pamphlebia rubrolimbraria* Guenée [1/1] (or); *Scopula emissaria* Walker [6/9] (or).

Hesperiidae: *Ampittia dioscorides* Fabricius [1/1] (or); *Ampittia dioscorides camertes* Hewitson [1/1] (or); *Ampittia dioscorides etura* Mabilie [1/1] (or); *Ancyloxypha numitor* Fabricius [1/8] (na); *Apaustus menes* Stoll [1/1] (nt); *Baoris pagana* de Nicéville [1/1] (or); *Borbo borbonica* Boisduval [1/5] (af); *Borbo cinnara* Wallace [1/15] (au; ia; or); *Borbo fanta* Evans [1/2] (af); *Borbo fatuellus* Hopffer [1/5] (af); *Borbo impar* Mabilie [1/1] (au); *Gegenes hottentota* Latreille [1/4] (af); *Gegenes niso* Linnaeus [1/4] (af); *Lerodea eufala* Edwards [1/9] (na; nt; nw); *Nyctelius nyctelius* Latreille [1/6] (nt); *Oriens gola* Moore [1/3] (or); *Panoquina ocola* Edwards [1/3] (na; nt); *Panoquina sylvicola*

Herrich-Schäffer [1/8] (nt); *Parnara amalia* Semper [1/2] (au); *Parnara bada sida* Waterhouse [1/2] (au); *Parnara ganga* Evans [1/2] (or); *Parnara guttatus* Bremer and Grey [2/9] (or; ow; pl); *Parnara guttatus apostata* Snellen [2/5] (or); *Parnara guttatus guttatus* Bremer and Grey [1/4] (or); *Parnara naso* Fabricius [2/3] (af; or); *Parnara naso bada* Moore [2/6] (au; or); *Parnara naso monasi* Trimen [1/1] (af); *Parnara poutieri* Boisduval [1/1] (af); *Pelopidas agna* Moore [1/3] (or); *Pelopidas agna agna* Moore [1/4] (or); *Pelopidas conjuncta* Herrich-Schäffer [1/7] (or; ow); *Pelopidas conjuncta conjuncta* Herrich-Schäffer [1/6] (or); *Pelopidas lyelli lyelli* Rothschild [1/3] (au); *Pelopidas mathias* Fabricius [3/11] (af; ia; or; ow); *Pelopidas mathias mathias* Fabricius [2/5] (or); *Perichares philetus* Gmelin [2/12] (nt); *Polytrems pellucida* Murray [1/1] (ow); *Potanthus dara* Kollar [1/3] (or); *Potanthus omaha* Edwards [2/8] (or); *Potanthus tropica* Plötz [1/1] (or); *Prosopalpus styła* Evans [1/1] (af); *Pseudoborbo bevani* Moore [3/6] (or); *Taractrocera ceramas* Hewitson [1/1] (or); *Taractrocera ina ina* Waterhouse [1/4] (au); *Taractrocera papyria papyria* Boisduval [2/11] (au); *Telicota augias* Linnaeus [1/5] (ia; or); *Telicota augias argilus* Waterhouse [1/1] (au); *Telicota bambusae* Moore [2/6] (au; or); *Telicota ohara* Plötz [1/2] (or); *Wallengrenia drury* Latreille [1/2] (nt); *Wallengrenia otho* Smith [1/4] (nt; nw); *Wallengrenia premnas* Wallengren [1/4] (nt).

Lasiocampidae: *Lenodora vittata* Walker [2/3] (or).

Limacodidae: *Parasa bicolor* Walker [1/3] (or); *Parasa lepida* Cramer [35/77] (ia; or; ow); *Thosea sinensis* Walker [15/18] (au; ia; or; ow).

Lymantriidae: *Cifuna locuples* Walker [6/12] (or; pl); *Euproctis varians* Walker [9/17] (or); *Euproctis virgo* Swinhoe [2/2] (or); *Laelia coenosa* Hübner [3/2] (or; pl); *Laelia fasciata* Moore [1/1] (or); *Laelia fracta* Schaus and Clement [3/4] (af); *Laelia rosea* Schaus and Clement [1/1] (af); *Laelia suffusa* Walker [2/6] (or); *Leucoma salicis* Linnaeus [4/5] (hl; na; pl); *Psalis pennatula* Fabricius [11/18] (af; or; ow); *Sphrageidus virguncula* Walker [12/25] (or); *Sphrageidus xanthorrhoea* Kollar [10/18] (or).

Noctuidae: *Achaea catocaloides* Guenée [12/14]

(af); *Acontia crocata* Guenée [2/3] (or); *Actebia fennica* Tauscher [25/47] (hl; na; pl); *Agrotis ipsilon* Hufnagel [30/74] (af; au; cm; hw; ia; na; nt; nz; or; ow; pl); *Agrotis longidentifera* Hampson [7/9] (af); *Agrotis repleta* Walker [11/20] (nt); *Agrotis subterranea* Fabricius [17/39] (na; nt; nw); *Aletia exsanguis* Guenée [1/2] (or); *Aletia panarista* Fletcher [1/1] (af); *Aletia umbrigerata* Saalmüller [1/1] (af); *Anicla ignicans* Guenée [4/10] (nt; pl); *Anticarsia gemmatilis* Hübner [4/21] (na; nt); *Anticarsia irrorata* Fabricius [4/16] (af; au; or; ow); *Ariathisa abyssinia* Guenée [4/5] (af; or); *Bathytricha truncata* Walker [4/7] (au); *Busseola fusca* Fuller [3/8] (af); *Chalciope alcyona* Druce [1/1] (au); *Cretonia vegetus* Swinhoe [2/2] (or); *Eublemma anachoresis* Wallengren [3/2] (af; au; or); *Faronta albilinea* Hübner [5/23] (na; nt; nw); *Faronta quadrannulata* Morrison [1/4] (nt); *Gnamptonyx innexa* Walker [1/1] (af); *Grammodes bifasciata* Petagna [4/4] (af; pl); *Grammodes geometrica* Fabricius [7/9] (af; or; ow); *Grammodes stolidata* Fabricius [8/9] (af; or; ow); *Helicoverpa armigera* Hübner [40/102] (af; au; cm; ia; na; nt; nz; or; ow; pl); *Helicoverpa zea* Boddie [38/111] (af; hw; na; nt; nw; or); *Hiccoda nigripalpis* Walker [1/1] (or); *Leucania albistigma* Moore [1/1] (or); *Leucania compta* Moore [1/1] (or); *Leucania humidicola* Guenée [1/6] (nt); *Leucania insularis* Butler [1/2] (or); *Leucania irregularis* Walker [1/3] (au; or); *Leucania jaliscana* Schaus [1/4] (nt); *Leucania latiuscula* Herrich-Schäffer [1/12] (na; nt); *Leucania loreyi* Duponchel [5/17] (af; au; or; ow; pl); *Leucania microsticha* Hampson [1/5] (nt); *Leucania phaea* Hampson [1/4] (af; pl); *Leucania polystrota* Hampson [1/4] (nt); *Leucania roseilinea* Walker [1/1] (or); *Leucania venalba* Moore [1/2] (au; or); *Maliattha signifera* Walker [1/1] (or); *Mocis frugalis* Fabricius [5/15] (af; au; ia; or); *Mocis latipes* Guenée [10/37] (na; nt; nw); *Mocis punctularis* Hübner [2/3] (af; nt); *Mocis repanda* Fabricius [6/5] (af; nt); *Mocis trifasciata* Stephens [2/6] (au); *Mythimna l-album* Linnaeus [1/2] (pl); *Mythimna vitellina* Hübner [2/2] (pl); *Mythimna zae* Duponchel [1/3] (ow); *Naranga aenescens* Moore [2/5] (or; ow); *Naranga diffusa* Walker [1/2] (or; ow); *Nodaria externalis* Guenée [2/2] (or); *Pandesma robusta* Walker [2/2] (af; or); *Plusia festucae* Linnaeus [2/4] (na; ow; pl); *Plusia putnami* Grote [4/6] (na; ow; pl); *Protodeltote distinguenda* Staudinger [1/1] (pl); *Pseudaletia*

adultera Schaus [4/14] (nt); *Pseudaletia separata* Walker [12/32] (au; ia; nz; or); *Pseudaletia unipuncta* Haworth [18/53] (au; cm; hw; na; nt; or; pl); *Rhododactyla elicrina* Felder [1/1] (af); *Rivula atimeta* Swinhoe [1/1] (or); *Rivula bioculalis* Moore [1/2] (or); *Rivula continentalis* Gaede [1/1] (af); *Rivula innotabilis* Swinhoe [1/1] (or); *Sciomesa biluma* Nye [1/3] (af); *Sesamia botanephaga* Tams and Bowden [3/10] (af); *Sesamia calamistis* Hampson [3/13] (af); *Sesamia cretica* Lederer [2/7] (af; or; ow; pl); *Sesamia inferens* Walker [3/24] (or; ow); *Sesamia nonagrioides* Lefèbvre [4/6] (af; ow; pl); *Sesamia penniseti* Tams and Bowden [1/8] (af); *Sesamia uniformis* Dudgeon [1/8] (ia; or); *Sesamia venosata* Moore [1/1] (or); *Simplicia robustalis* Guenée [5/9] (au; ia; or); *Simyra albovenosa* Goeze [10/21] (hl; or; ow; pl); *Speia vuteria* Stoll [3/8] (nt; ow); *Spodoptera cilium* Guenée [4/8] (af; or; ow; pl); *Spodoptera compta* Walker [1/5] (or); *Spodoptera exempta* Walker [7/29] (af; au; hw; or; ow); *Spodoptera exigua* Hübner [35/83] (af; au; cm; hw; na; or; pl); *Spodoptera frugiperda* Smith [34/91] (af; cm; na; nt; nw); *Spodoptera littoralis* Boisduval [25/43] (af; na; or; ow; pl); *Spodoptera litura* Fabricius [69/166] (af; au; cm; ia; nt; or; ow); *Spodoptera mauritia* Boisduval [7/20] (af; au; cm; hw; ia; or; ow); *Spodoptera pecten* Guenée [7/15] (ia; or); *Spodoptera praefica* Grote [16/35] (na); *Spodoptera triturrata* Walker [1/3] (af); *Trichoplusia indicator* Walker [1/1] (af); *Xanthodes graellsii* Feisthamel [3/10] (af; or; ow).

Nolidae: *Earias cupreoviridis* Walker [4/10] (af; au; or; ow); *Nola squalida* Staudinger [4/4] (ia; or).

Notodontidae: *Antheua woerdeni* Snellen [2/2] (af); *Phalera combusta* Walker [1/4] (or).

Nymphalidae: *Acraea terpsichore* Linnaeus [6/11] (af); *Bicyclus dorothea* Cramer [1/1] (af); *Bicyclus vulgaris* Butler [1/1] (af); *Junonia almana* Linnaeus [11/22] (ia; or; pl); *Junonia atlites* Linnaeus [6/14] (ia; or); *Junonia sophia* Fabricius [2/8] (af); *Melanitis leda* Linnaeus [2/33] (af; au; or; ow; pl); *Melanitis leda ismene* Cramer [1/4] (or); *Melanitis leda leda* Linnaeus [1/4] (or); *Melanitis phedima* Cramer [2/18] (or; pl); *Minois dryas* Scopoli [1/10] (or; pl); *Mycalesis gotama* Moore [1/9] (or; ow; pl); *Mycalesis gotama nanda* Fruhstorfer [1/9] (or); *Mycalesis horsfieldi* Moore [1/3] (or); *Mycalesis mamerta* Stoll [1/1] (or); *Mycalesis mineus* Linnaeus [1/8] (or); *Mycalesis*

nr. lorna Grose-Smith [1/1] (au); *Mycalesis perseus* Fabricius [1/13] (au; or; pl); *Mycalesis terminus* Fabricius [2/8] (au); *Mycalesis visala andamana* Moore [1/1] (or); *Orsotriaena medus cinerea* Butler [1/1] (or); *Orsotriaena medus mandata* Moore [1/1] (or); *Orsotriaena medus medus* Fabricius [1/1] (or); *Vanessa cardui* Linnaeus [25/104] (af; au; cm; hw; na; or; pl).

Psychidae: *Brachycyttarus griseus* Joannis [5/6] (or); *Mahasena graminivora* Hampson [2/3] (or).

Pterophoridae: *Exelastis atomosa* Walsingham [2/6] (af; or; ow).

Pyralidae: *Achyra coelatalis* Walker [1/3] (af; or); *Adelpherupa flavescens* Hampson [1/1] (af); *Aglossa dimidiatus* Haworth [2/2] (pl); *Ancylolomia chrysographellus* Kollar [1/3] (or); *Ancylolomia indica* Felder and Rogenh. [1/2] (or); *Ancylolomia inornata* Staudinger [1/3] (af); *Ancylolomia japonica* Zeller [1/1] (ow); *Ancylosis convexella* Lederer [1/1] (af); *Antigastra catalaunalis* Duponchel [5/7] (af; au; cm; or); *Bleszynskia malacelloides* Bleszynski [1/1] (or); *Bleszynskia malacellus* Duponchel [2/5] (af; au; ow); *Bradina admixtalis* Walker [2/2] (af; ow); *Cadra calidella* Guenée [8/10] (af; na; or; pl); *Cadra cautella* Walker [35/61] (af; au; cm; na; nt; or); *Carectocultus bivitta* Möschler [1/1] (nt); *Catagela adjurella* Walker [1/1] (or); *Chilo agamemnon* Bleszynski [1/5] (af; ow); *Chilo aleniella* Strand [1/1] (af); *Chilo auricilia* Dudgeon [1/9] (au; or); *Chilo christophi* Bleszynski [1/2] (pl); *Chilo diffusilinea* Joannis [1/4] (af); *Chilo infuscatellus* Snellen [1/3] (au; ia; or; ow); *Chilo nr. partellus* Swinhoe [1/1] (or); *Chilo partellus* Swinhoe [1/7] (af; or; ow); *Chilo phragmitellus* Hübner [1/2] (pl); *Chilo plejadellus* Zincken [1/1] (na; or); *Chilo polychrysa* Meyrick [2/11] (au; or; pl); *Chilo sacchariphagus* Bojer [1/7] (af; or; ow); *Chilo suppressalis* Walker [3/19] (af; au; hw; ia; na; or; ow); *Chilo zacconius* Bleszynski [1/5] (af); *Cnaphalocrocis bilinealis* Hampson [1/1] (or); *Cnaphalocrocis exigua* Butler [1/4] (au; ia; or); *Cnaphalocrocis medinalis* Guenée [4/14] (au; or; ow); *Cnaphalocrocis patnalis* Bradley [2/7] (or); *Cnaphalocrocis poeyalis* Boisduval [1/1] (au; ia); *Cnaphalocrocis trapezalis* Guenée [1/14] (af; au; cm; na; nt; or); *Coniesta ignefusalis* Hampson [1/4] (af); *Corcyra cephalonica* Stainton [19/39] (af; cm; hw; na; nt; or); *Crypsiptya coclesalis* Walker [4/12]

(or; ow); *Cryptoblabes gnidiella* Millière [30/49] (af; cm; hw; na; nt; or; pl); *Diatraea lineolata* Walker [1/5] (nt; nw); *Diatraea saccharalis* Fabricius [2/19] (na; nt; nw; or); *Doloessa viridis* Zeller [10/12] (or); *Donacaula dodatellus* Walker [2/2] (or); *Donacaula forficella* Thunberg [2/4] (or; pl); *Elasmopalpus lignosellus* Zeller [23/38] (cm; na; nt; nw); *Eldana saccharina* Walker [3/8] (af); *Elophila difflualis* Snellen [5/5] (or; ow; pl); *Elophila nymphaeata* Linnaeus [6/7] (pl); *Endotricha melanobasis* Hampson [1/1] (or); *Endotricha puncticostalis* Walker [2/2] (au; or); *Eoreuma loftini* Dyar [1/6] (na); *Ephestia elutella* Hübner [15/17] (cm; na; nt; or; pl); *Ephestia kuehniella* Zeller [12/21] (hl; na; nt; pl); *Epina dichromella* Walker [1/1] (or); *Eurrhyarodes bracteolalis* Zeller [2/2] (or); *Herpetogramma licarsisalis* Walker [6/15] (af; au; or; ow); *Mabra eryxalis* Walker [1/1] (or); *Maliarpha separatella* Ragonot [1/2] (af; ow); *Marasmia ruralis* Walker [1/1] (or); *Marasmia venialis* Walker [1/8] (af; au; ia; or); *Maruca vitrata* Fabricius [6/16] (cm; na; or); *Metoeca foederalis* Guenée [1/1] (or); *Monoctenocera brachiella* Hampson [2/6] (or); *Niphadoses palleucus* Common [1/1] (au); *Nymphula ussuriensis* Rebel [1/1] (pl); *Panalipa immeritalis* Walsingham [1/1] (or); *Paralipsa gularis* Zeller [22/28] (hl; hw; na); *Parapoinx diminutalis* Snellen [5/6] (hl; na; nt; or; pl); *Parapoinx fluctuosalis* Zeller [3/3] (au; cm; hw; nt; or; ow); *Parapoinx indomitalis* Berg [1/1] (nt); *Parapoinx stagnalis* Zeller [3/3] (af; or; ow); *Parapoinx vittalis* Bremer [2/2] (pl); *Parerupa africana* Aurivillius [1/1] (af); *Plodia interpunctella* Hübner [25/48] (af; cm; na; nt; or; pl); *Psara basalis* Walker [7/11] (af; or; ow); *Rupela albina* Becker and Solis [1/1] (nt); *Saluria inficita* Walker [1/3] (or); *Sameodes cancellalis* Zeller [3/3] (af; or); *Scirpophaga excerptalis* Walker [1/3] (ia; or); *Scirpophaga gilviberbis* Zeller [1/1] (af; or); *Scirpophaga incertulas* Walker [2/10] (or; ow); *Scirpophaga innotata* Walker [2/2] (au; ia; or); *Scirpophaga melanoclista* Meyrick [1/1] (af); *Scirpophaga nivella* Fabricius [2/6] (or; ow); *Scirpophaga subumbrosa* Meyrick [1/1] (af); *Tatobotys biannulalis* Walker [2/2] (au); *Zovax vangoghi* Bleszynski [1/1] (af).

Sphingidae: *Macroglossum trochilus trochiloides* Butler [1/1] (af).

Thyrididae: *Opula spilotata* Warren [1/1] (af).

Tineidae: *Haplotinea ditella* Pierce and Diak. [2/3] (pl); *Setomorpha rutella* Zeller [19/23] (af; au; cm; ia; na; nt; or; ow).

Zygaenidae: *Balataea zebraica* Butler [1/2] (or).

MALVACEAE

Gossypium barbadense

Cosmopterigidae: *Pyroderces falcata* Stainton [8/10] (au; or); *Pyroderces ptilodelta* Meyrick [5/7] (or); *Pyroderces rileyi* Walsingham [13/18] (au; hl; hw; na; nt; or); *Pyroderces simplex* Walsingham [11/17] (af; cm; or; ow; pl).

Cossidae: *Zeuzera coffeae* Nietner [33/79] (au; ia; or).

Gelechiidae: *Pectinophora gossypiella* Saunders [6/14] (af; au; cm; hw; ia; na; nt; or; ow; pl).

Gracillariidae: *Phyllonorycter triarcha* Meyrick [1/1] (af; or).

Nepticulidae: *Stigmella gossypii* Forbes [1/2] (nt; nw).

Noctuidae: *Agrotis subterranea* Fabricius [17/39] (na; nt; nw); *Alabama argillacea* Hübner [3/5] (na; nt; nw); *Anomis erosa* Hübner [9/21] (af; au; cm; ia; na; nt; or); *Anomis flava* Fabricius [9/22] (af; au; cm; na; nt; or; ow); *Anomis impasta* Guenée [1/4] (na; nt; nw); *Anomis luridula* Guenée [1/1] (nt); *Anomis vulpina* Butler [1/3] (au); *Condica concisa* Walker [3/2] (na; nt; or); *Elaphria agrotina* Guenée [3/3] (nt); *Helicoverpa armigera* Hübner [40/102] (af; au; cm; ia; na; nt; nz; or; ow; pl); *Heliothis virescens* Fabricius [19/50] (na; nt; nw); *Neogalea sunia* Guenée [8/11] (au; cm; hw; na; nt); *Spodoptera dolichos* Fabricius [14/22] (na; nt); *Spodoptera frugiperda* Smith [34/91] (af; cm; na; nt; nw); *Spodoptera latifascia* Walker [16/24] (na; nt; nw); *Spodoptera pulchella* Herrich-Schäffer [1/1] (nt); *Trichoplusia ni* Hübner [27/65] (af; cm; hw; na; nt; or; pl).

Nolidae: *Earias huegeli* Rogenhofer [2/3] (au; ia); *Earias insulana* Boisduval [9/22] (af; au; or; ow; pl); *Earias vitella* Fabricius [1/10] (au; ia; or).

Pyralidae: *Haritalodes derogata* Fabricius [10/24] (af; au; cm; or; ow).

Saturniidae: *Citheronia regalis* Fabricius [18/23] (na).

Tortricidae: *Adoxophyes fasciculana* Walker [26/43] (au; or).

Gossypium hirsutum

Cosmopterigidae: *Pyroderces rileyi* Walsingham [13/18] (au; hl; hw; na; nt; or).

Gelechiidae: *Pectinophora gossypiella* Saunders [6/14] (af; au; cm; hw; ia; na; nt; or; ow; pl).

Nepticulidae: *Stigmella gossypii* Forbes [1/2] (nt; nw).

Noctuidae: *Agrotis ipsilon* Hufnagel [30/74] (af; au; cm; hw; ia; na; nt; nz; or; ow; pl); *Alabama argillacea* Hübner [3/5] (na; nt; nw); *Anomis erosa* Hübner [9/21] (af; au; cm; ia; na; nt; or); *Anomis illita* Guenée [2/11] (nt; ow); *Anomis impasta* Guenée [1/4] (na; nt; nw); *Helicoverpa armigera* Hübner [40/102] (af; au; cm; ia; na; nt; nz; or; ow; pl); *Helicoverpa zea* Boddie [38/111] (af; hw; na; nt; nw; or); *Heliothis virescens* Fabricius [19/50] (na; nt; nw); *Neogalea sunia* Guenée [8/11] (au; cm; hw; na; nt); *Spodoptera eridania* Stoll [31/63] (na; nt; nw); *Spodoptera latifascia* Walker [16/24] (na; nt; nw); *Spodoptera ornithogalli* Guenée [25/53] (cm; na; nt).

Pyralidae: *Achyra rantalis* Guenée [8/14] (na; nt; nw); *Ephesiodes gilvescentella* Ragonot [4/7] (na; nw); *Euzophera semifuneralis* Walker [13/18] (na; nw); *Moodna ostrinella* Clemens [9/13] (na; nw); *Paralipsa gularis* Zeller [22/28] (hl; hw; na).

Tortricidae: *Amorbia phaseolana* Busck [4/6] (nt); *Platynota rostrana* Walker [25/42] (na; nt; nw).

Gossypium tomentosum

Bucculatricidae: *Bucculatrix thurberiella* Busck [1/2] (hw; na; nt; nw).

Gelechiidae: *Pectinophora gossypiella* Saunders [6/14] (af; au; cm; hw; ia; na; nt; or; ow; pl).

REFERENCES

- Acciarri N, Vitelli G, Arpaia S, Mennella G, Sunseri F, Rotino GL (2000) Transgenic resistance to the Colorado potato beetle in *Bt* expressing eggplant fields. *Hortscience* **35**: 722
- Agrawal AA (1999) Induced responses to herbivory in wild radish: Effects on several herbivores and plant fitness. *Ecology* **80**: 1713
- Agrawal AA, Strauss SY, Stout MJ (1999) Costs of induced responses and tolerance to herbivory in male and female fitness components of wild radish. *Evolution* **53**: 1093
- Alstad DN, Andow DA (1995) Managing the evolution of resistance to transgenic plants. *Science* **268**: 1894
- Andow DA (2002) Resisting resistance to *Bt* crops. In Letourneau DK, Burrows BE, eds, Genetically Engineered Organisms: Assessing Environmental and Human Health Effects. CRC Press, Boca Raton, FL, pp 99–121
- Archer TL, Schuster G, Patrick C, Cronholm G, Bynum ED, Morrison WP (2000) Whorl and stalk damage by European and Southwestern corn borers to four events of *Bacillus thuringiensis* transgenic maize. *Crop Protection* **19**: 181
- Ashfaq M, Young SY, McNew RW (2000) Development of *Spodoptera exigua* and *Helicoverpa zea* (Lepidoptera: Noctuidae) on transgenic cotton containing CryIac insecticidal protein. *J. Entomol. Sci.* **35**: 360
- Barbosa P (1993) Lepidopteran foraging on plants in agroecosystems: Constraints and consequences. In Stamp NE, Casey TM, eds, Ecological and Evolutionary Constraints on Foraging Caterpillars, pp 29
- Barbosa P (1998) ed, Conservation Biological Control. Academic Press
- Benbrook CM, Groth E, Halloran JM, Hansen MK, Marquardt S (1996) Pest Management at the Crossroads. Consumers Union, Yonkers, New York
- Bergelson J (1994) Changes in fecundity do not predict invasiveness: A model study of transgenic plants. *Ecology* **75**: 249
- Bergelson J, Purrington CB (2002) Factors affecting the spread of resistant *Arabidopsis thaliana* populations. In Letourneau DK, Burrows BE, eds, Genetically Engineered Organisms: Assessing Environmental and Human Health Effects. CRC Press, Boca Raton, FL, pp 33
- Betz FS, Hammond BG, Fuchs RL (2000) Safety and advantages of *Bacillus thuringiensis*-protected plants to control insect pests. *Regul. Toxicol. Pharmacol.* **32**: 156–173
- Bourget D, Bethenod MT, Trouve C, Frederique V (2000) Host-plant diversity of the European corn borer *Ostrinia nubilalis*: What value for sustainable transgenic insecticidal *Bt* maize? *Proc. R. Soc. Lond. B Biol. Sci.* **267**: 1177
- Callaway RM, DeLuca TH, Belliveau WM (1999) Biological-control herbivores may increase competitive ability of the noxious weed *Centaurea maculosa*. *Ecology* **80**: 1196–1201
- Caswell H (2001) Matrix Population Models. Sinauer, Sunderland, Massachusetts
- Chèvre AM, Eber F, Baranger A, Hureau G, Barret P, Picault H, Renard M (1998) Characterization of backcross generations obtained under field conditions from oilseed rape wild radish F-1 interspecific hybrids – An assessment of transgene dispersal. *Theor. Appl. Genet.* **97**: 90–98
- Colwell RK, Norse EA, Pimentel D, Sharples FE, Simberloff D (1985) Genetic engineering in agriculture. *Science* **229**: 111
- Crawley M, Harvey PH, Purvis A (1996) Comparative ecology of the native and alien floras of the British Isles.

- Philos. Trans. R. Soc. Lond. B Biol. Sci.* **351**: 1251
- Daehler CC, Strong DR** (1996) Status, prediction and prevention of introduced cordgrass *Spartina* spp. Invasions in Pacific Estuaries, USA. *Biol. Conserv.* **78**: 51–58
- Darmency H** (1994) The impact of hybrids between genetically modified crop plants and their related species – Introgression and weediness. *Mol. Ecol.* **3**: 37–40
- Doak DF** (1991) The consequences of herbivory for dwarf fireweed: Different time scales, different morphological scales. *Ecology* **72**: 1397
- Doak DF** (1992) Lifetime impacts of herbivory for a perennial plant. *Ecology* **73**: 2086–2099
- Dyer LA, Letourneau DK** (1999) Trophic cascades in a complex terrestrial community. *Proc. Natl. Acad. Sci. USA* **96**: 5072–5076
- Ellstrand NC, Prentice HC, Hancock JF** (1999) Gene flow and introgression from domesticated plants into their wild relatives. *Annu. Rev. Ecol. Syst.* **30**: 539–563
- Felton GW, Dahlman DL** (1984) Allelochemical Induced Stress – Effects of L-canavanine on the pathogenicity of *Bacillus thuringiensis* in *Manduca sexta*. *J. Invertebr. Pathol.* **44**: 187–191
- Fitton MG, Shaw MR, Gauld ID** (1988) Pimpline ichneumonflies, Hymenoptera, Ichneumonidae (Pimplinae). *Handbook for the Identification of British Insects* **7**: 1
- Fretwell SD** (1977) The regulation of plant communities by food chains exploiting them. *Perspect. Biol. Med.* **20**: 169
- Geervliet JBF, Posthumus MA, Vet LEM, Dicke M** (1997) Comparative analysis of headspace volatiles from different caterpillar-infested or uninfested food plants of *Pieris* species. *J. Chem. Ecol.* **23**: 2935–2954
- Hails RS** (2000) Genetically modified plants – The debate continues. *Trends. Ecol. Evol.* **15**: 14–18
- Hauser TP, Shaw RG, Ostergard H** (1998) Fitness of F-1 hybrids between weedy *Brassica rapa* and oilseed rape (*B. napus*). *Heredity* **81**: 429–435
- Hedin PA, Lindig OH, Sikorowski PP, Wyatt M** (1978) Suppressants of gut bacteria in the boll weevil from the cotton plant. *J. Econ. Entomol.* **71**: 394–396
- Hellmich RL, Siegfried BD, Sears MK, Stanley-Horn DE, Daniels MJ, Mattila HR, Spencer T, Bidne KG, Lewis LC** (2001) Monarch larvae sensitivity to *Bacillus thuringiensis*-purified proteins and pollen. *Proc. Natl. Acad. Sci. USA* **98**: 11925–11930
- Hilbeck A** (2002) Transgenic host plant resistance and non-target effects. In Letourneau DK, Burrows BE, eds, Genetically engineered organisms: assessing environmental and human health effects. CRC Press, Boca Raton, Florida, pp 33
- Hoffman CA** (1990) Ecological risks of genetic engineering of crop plants: scientific and social analyses are critical to realize benefits of the new techniques. *Bioscience* **40**: 434
- Hull LA, Beers EH** (1985) Ecological selectivity: modifying chemical control practices to preserve natural enemies. In Hoy MA, Herzog DC, eds, Biological Control in Agricultural IPM Systems. Academic Press, Inc., New York
- James RR, Miller JC, Lighthart B** (1993) *Bacillus thuringiensis* var. *kurstaki* affects a beneficial insect, the cinnabar moth (Lepidoptera: Arctiidae). *J. Econ. Entomol.* **86**: 334
- Jenczewski E, Ronfort J, Chèvre AM** (2003) Crop-to-wild gene flow, introgression and possible fitness effects of transgenes. *Environ. Biosafety Res.* **2**: 9–24
- Jesse LCH, Obrycki JJ** (2000) Field deposition of *Bt* transgenic corn pollen: lethal effects on the monarch butterfly. *Oecologia* **125**: 241–248
- Johnson KS, Scriber JM, Nitao JK, Smitley DR** (1995) Toxicity of *Bacillus thuringiensis* var. *kurstaki* to three nontarget lepidoptera in field studies. *Environ. Entomol.* **24**: 288–297
- Jørgensen RB, Andersen B** (1994) Spontaneous hybridization between oilseed rape (*Brassica napus*) and weedy *Brassica campestris* (Brassicaceae) – a rise of growing genetically-modified oilseed rape. *Am. J. Bot.* **81**: 1620–1626
- Jørgensen RB, Andersen B, Landbo L, Mikkelsen TR, Dias JS, Crute I, Monteiro AA** (1996) Spontaneous hybridization between oilseed rape (*Brassica napus*) and weedy relatives. *Acta Hort.* **407**: 193
- Juenger T, Bergelson J** (1998) Pairwise *versus* diffuse natural selection and the multiple herbivores of scarlet gilia, *Ipomopsis aggregata*. *Evolution* **52**: 1583–1592
- Kareiva P, Morris W, Jacobi CM** (1994) Studying and managing the risk of cross-fertilization between transgenic crops and wild relatives. *Mol. Ecol.* **3**: 15–21
- Kareiva P, Parker IM, Pascual M** (1996) Can we use experiments and models in predicting the invasiveness of genetically engineered organisms. *Ecology* **77**: 1670–1675
- Klinger T** (2002) Variability and uncertainty in crop-to-wild hybridization. In Letourneau DK, Burrows BE, eds, Genetically engineered organisms: assessing environmental and human health effects. CRC Press, Boca Raton, Florida, pp 1
- Klinger T, Ellstrand NC** (1994) Engineered genes in wild populations – Fitness of weed-crop hybrids of *Raphanus sativus*. *Ecol. Appl.* **4**: 117–120
- Koptur S** (1990) Early season defoliation can affect *Carex laxiflora* Cyperaceae seed set in same year or reproductive allocation in subsequent years. *Bull. Ecol. Soc. Am.* **71**: 217
- Krishik VA, Barbosa P, Reichelderfer CF** (1988) Three trophic level interactions: allelochemicals, *Manduca sexta*, and *Bacillus thuringiensis* var. *kurstaki* Berliner. *Environ. Entomol.* **17**: 476–482
- Kriticos D, Brown J, Radford I, Nicholas M** (1999) Plant population ecology and biological control: *Acacia nilotica* as a case study. *Biol. Control.* **16**: 230–239
- Lefol E, Seguinswarts G, Downey RK** (1997) Sexual hybridisation in crosses of cultivated *Brassica* species with the crucifers *Erucastrum gallicum* and *Raphanus raphanistrum* –

- Potential for gene introgression. *Euphytica* **95**: 127–139
- Letourneau DK, Hagen JA, Robinson GS** (2002) *Bt* crops: Evaluating benefits under cultivation and risks from escaped transgenes in the wild. In Letourneau DK, Burrows BE, eds, *Genetically Engineered Organisms: Assessing Environmental and Human Health Effects*. CRC Press, Boca Raton, Florida, pp 33
- Losey JE, Obrycki JJ, Hufbauer RA** (2002) Impacts of genetically engineered crops on non-target herbivores: *Bt* corn and monarch butterflies as a case study. In Letourneau DK, Burrows BE, eds, *Genetically Engineered Organisms: Assessing Environmental and Human Health Effects*. CRC Press, Boca Raton, Florida, pp 143
- Losey JE, Rayor LS, Carter ME** (1999) Transgenic pollen harms monarch butterflies. *Nature* **399**: 214
- Louda SM** (1999) Insect limitation of weedy plants and its implications. In Traynor PL, Westwood JH, eds, *Conference Proceedings: Workshop on Ecological Effects of Pest Resistance Genes in Managed Ecosystems*. Information Systems for Biotechnology, Bethesda, Maryland
- Macintosh SC, Stone TB, Sims SR, Hunst PL, Greenplate JT, Marrone PG, Perlak J, Fischhoff DA, Fuchs RL** (1990) Specificity and efficacy of purified *Bacillus thuringiensis* proteins against agronomically important insects. *J. Invertebr. Pathol.* **56**: 258
- Maron JL** (1998) Insect Herbivory above- and below-ground – Individual and joint effects on plant fitness. *Ecology* **79**: 1281–1293
- Marquis RJ** (1984) Leaf herbivores decrease fitness of a tropical plant. *Science* **226**: 537
- Marquis RJ** (1992) A bite is a bite is a bite? Constraints on response to folivory in *Piper arietinum* (Piperaceae). *Ecology* **73**: 143–152
- Marvier M, Kareiva P** (1999) Extrapolating from field experiments that remove herbivores to population-level effects of herbivore-resistant transgenes. In Traynor PL, Westwood JH, eds, *Conference Proceedings: Workshop on Ecological Effects of Pest Resistance Genes in Managed Ecosystems*. Information Systems for Biotechnology, Blacksburg, Virginia, <http://www.nbiap.vt.edu>
- Mauricio R, Bowers MD, Bazzaz FA** (1993) Pattern of leaf damage affects fitness of the annual plant *Raphanus sativus* (Brassicaceae). *Ecology* **74**: 2066–2071
- McCall PJ, Turlings TCJ, Loughrin J, Proveaux AT, Tumlinson JH** (1994) Herbivore-induced volatile emissions from cotton (*Gossypium hirsutum* L.) seedlings. *J. Chem. Ecol.* **20**: 3039–3050
- McNaughton SJ** (1986) On plants and herbivores. *Am. Nat.* **128**: 765
- Messeguer J, Fogher C, Guiderdoni E, Marfa V, Catala MM, Baldi G, Mele E** (2001) Field assessments of gene flow from transgenic to cultivated rice (*Oryza sativa* L.) using a herbicide resistance gene as tracer marker. *Theor. Appl. Genet.* **103**: 1151–1159
- Meyer GA** (2000) Interactive effects of soil fertility and herbivory on *Brassica nigra*. *Oikos* **88**: 433–441
- Mikkelsen TR, Jensen J, Jorgensen RB** (1996) Inheritance of oilseed rape (*Brassica napus*) RAPD markers in a backcross progeny with *Brassica campestris*. *Theor. Appl. Genet.* **92**: 492–497
- Mullin CA, Croft BA** (1985) An update on development of selective pesticides favoring arthropod natural enemies. In Hoy MA, Herzog DC, eds, *Biological Control in Agriculture IPM Systems*. Academic Press, Inc., New York
- Naber AC, Aarssen LW** (1998) Effects of shoot apex removal and fruit herbivory on branching, biomass and reproduction in *Verbascum thapsus* (Scrophulariaceae). *Am. Midl. Nat.* **140**: 42–54
- National Research Council** (2000) *Genetically Modified Pest-Protected Plants: Science and Regulation*. National Academy Press, Washington DC
- National Research Council** (2002) *Environmental Effects of Transgenic Plants: The scope and adequacy of regulation*. National Academy Press, Washington DC
- Navon A** (1993) Control of lepidopteran pests with *Bacillus thuringiensis*. In Entwistle PF, Cory S, Bailey MJ, Higgs S, eds, *Bacillus thuringiensis*, an environmental biopesticide: theory and practice. Wiley, Chichester England, New York, pp 311
- Neeser C** (1999) Report of the *Brassica* crops working group. In Traynor PL, Westwood JH, eds, *Conference Proceedings: Workshop on Ecological Effects of Pest Resistance Genes in Managed Ecosystems*. Information Systems for Biotechnology, Bethesda, Maryland
- Obrycki JJ, Losey JE, Taylor OR, Jesse LCH** (2001) Transgenic insecticidal corn: Beyond insecticidal toxicity to ecological complexity. *Bioscience* **51**: 353–361
- Parker IM** (2000) Invasion dynamics of *Cytisus scoparius*: A matrix model approach. *Ecol. Appl.* **10**: 726–743
- Paulison MA** (1987) Exploitation by, and the effects of, caterpillar grazers on the annual, *Rudbeckia hirta* (Compositae). *Am. Midl. Nat.* **117**: 439
- Peacock JW, Schweitzer DF, Carter JL, Dubois NR** (1998) Laboratory assessment of the effects of *Bacillus thuringiensis* on native Lepidoptera. *Environ. Entomol.* **27**: 450–457
- Peferoen M** (1997) Progress and prospects for field use of *Bt* genes in crops. *Trends Biotechnol.* **15**: 173–177
- Peterson G, Cunningham S, Deutsch L, Erickson J, Quinlan A, Raez-Luna E, Tinch R, Troell M, Woodbury P, Zens S** (2000) The risks and benefits of genetically modified crops: A multidisciplinary perspective. *Conserv. Ecol.* **4**: 38–49
- Phipps RH, Park JR** (2002) Environmental benefits of genetically modified crops: Global and European perspectives on their ability to reduce pesticide use. *J. Anim. Feed. Sci.* **11**: 1–18
- Pilson D** (1996) Two herbivores and constraints on selection for resistance in *Brassica rapa*. *Evolution* **50**: 1492

- Pilson D** (2000) Herbivory and natural selection on flowering phenology in wild sunflower, *Helianthus annuus*. *Oecologia* **122**: 72–82
- Pilson D, Decker KL** (2002) Compensation for herbivory in wild sunflower: Response to simulated damage by the head-clipping weevil. *Ecology* **83**: 3097–3107
- Price PW** (1992) Plant resources as the mechanistic basis for insect herbivore population dynamics. In Hunter MD, Ohgushi T, Price PW, eds, *Effects of Resource Distribution on Animal-Plant Interactions*. Academic Press, San Diego, California, pp 139
- Reichelderfer CF** (1991) Interactions among allelochemicals, some Lepidoptera, *Bacillus thuringiensis* Berliner. In Barbosa B, Kirschik VA, Jones CG, eds, *Microbial Mediation of Plant-Herbivore Interactions*. Wiley Press, New York
- Robinson GS** (1998) Bugs, hollow curves and species-diversity indexes. *STATS – American Statistical Association* **21**
- Robinson GS** (1999) HOSTS – A database of the hostplants of the world's Lepidoptera. *Nota Lepidopterologica* **22**: 35
- Robinson GS, Ackery PR, Kitching IJ, Beccaloni GW, Hernandez LM** (2001) Hostplants of the moth and butterfly caterpillars of the oriental region. Southdene Sdn Bhd, Kuala Lumpur
- Robinson GS, Ackery PR, Kitching IJ, Beccaloni GW, Hernandez LM** (2002a) Hostplants of the moth and butterfly caterpillars of America north of Mexico. *Mem. Am. Entomol. Inst.* **69**: 1–824
- Robinson GS, Ackery PR, Kitching IJ, Beccaloni GW, Hernandez LM** (2002b) HOSTS – A database of hostplants of the world's Lepidoptera, <http://www/nhm.ac.uk/entomology/hostplants/index.html>
- Royal Society of Canada** (2001) An Expert Panel Report on the Future of Food Biotechnology. The Royal Society of Canada, Ottawa, Canada
- Saxena D, Flores S, Stotzky G** (1999) Insecticidal toxin in root exudates from *Bt* corn. *Nature* **402**: 480
- Schuster MR, Calderon M** (1986) Interactions of host plant resistant genotypes and beneficial insects in cotton ecosystems. In Boethel DJ, Eikenbary RD, eds, *Interaction of Host Plant Resistance and Parasitoids and Predators of Insects*. Halstead Press, New York, pp 84–97
- Sears MK, Hellmich RL, Stanley-Horn DE, Oberhauser KS, Pleasants JM, Mattila HR, Siegfried BD, Dively GP** (2001) Impact of *Bt* corn pollen on monarch butterfly populations: A risk assessment. *Proc. Natl. Acad. Sci. USA* **98**: 11937–11942
- Shea K, Kelly D** (1998) Estimating biocontrol agent impact with matrix models: *Carduus nutans* in New Zealand. *Ecol. Appl.* **8**: 824–832
- Smith RA, Couche GA** (1991) The phylloplane as a source of *Bacillus thuringiensis* variants. *Appl. Environ. Microbiol.* **57**: 311
- Snow AA, Andersen B, Jorgensen RB** (1999) Costs of transgenic herbicide resistance introgressed from *Brassica napus* into weedy *B. rapa*. *Mol. Ecol.* **8**: 605–615
- Snow AA, Palma PM** (1997) Commercialization of transgenic plants: Potential ecological risks. *Bioscience* **47**: 206–206
- Snow AA, Pilson D, Rieseberg LH, Paulsen MJ, Pleskac N, Reagon MR, Wolf DE, Selbo SM** (2003) A *Bt* transgene reduces herbivory and enhances fecundity in wild sunflowers. *Ecol. Appl.* **13**: 279–286
- Song ZP, Lu BR, Zhu YG, Chen JK** (2003) Gene flow from cultivated rice to the wild species *Oryza rufipogon* under experimental field conditions. *New Phytol.* **157**: 657–665
- Srinivasan G, Babu PC** (2001) Effects of *Bacillus thuringiensis* Berliner on predatory green lacewing, *Chrysoperla carnea* Stephens (Chrysopidae: Neuroptera). *Pestic Res. J.* **13**: 266–269
- Stewart CN, All JN, Raymer PL, Ramachandran S** (1997) Increased fitness of transgenic insecticidal rapeseed under insect selection pressure. *Mol. Ecol.* **6**: 773–779
- Story JM, Good WR, White LJ, Smith L** (2000) Effects of the interaction of the biocontrol agent *Agapeta zoegana* L. (Lepidoptera: Cochylidae) and grass competition on spotted knapweed. *Biol. Control* **17**: 182–190
- Strauss SY, Siemens DH, Decher MB, Mitchell-Olds T** (1999) Ecological costs of plant resistance to herbivores in the currency of pollination. *Evolution* **53**: 1105–1113
- Strong DR** (1984) Density-vague ecology and liberal population regulation in insects. In Price PW, Slobodchikoff CN, Gaud WS, eds, Wiley, New York, pp 313
- Strong DR** (1992) Are trophic cascades all wet – Differentiation and donor-control in speciose ecosystems. *Ecology* **73**: 747–754
- Tiedje JM, Colwell RK, Grossman YL, Hodson RE, Lenski RE, Mack RN, Regal PJ** (1989) The planned introduction of genetically engineered organisms: ecological considerations and recommendations. *Ecology* **70**: 298
- Tscharntke T** (1999) Insects on common reed (*Phragmites australis*): community structure and the impact of herbivory on shoot growth. *Aquat. Bot.* **64**: 399–410
- Turkington R, Klein E, Chanway CP** (1993) Interactive effects of nutrients and disturbance – an experimental test of plant strategy theory. *Ecology* **74**: 863–878
- Turlings TCJ, Bernasconi M, Bertossa R, Bigler F, Caloz G, Dorn S** (1998) The induction of volatile emissions in maize by three herbivore species with different feeding habits – Possible consequences for their natural enemies. *Biol. Control* **11**: 122–129
- UN** (1935) Genome-analysis in *Brassica* with special reference to the experimental formation of *B. napus* and peculiar mode of fertilization. *Jap. J. Bot.* **7**: 389–452
- van Frankenhuyzen K, Nystrom C** (1999) The *Bacillus thuringiensis* toxin specificity database. <http://www.glfccfs.nrcan.gc.ca/bacillus>
- van Frankenhuyzen K, Gringorten JL, Milne RE, Gauthier D, Pusztai M, Brousseau R, Masson L** (1991) Specificity of activated Cry1a proteins from *Bacillus thuringiensis* subsp.

- kurstaki* Hd-1 for defoliating forest Lepidoptera. *Appl. Environ. Microbiol.* **57**: 1650–1655
- Volenberg DS, Hopen HJ, Campobasso G** (1999) Biological control of yellow toadflax (*Linaria vulgaris*) by *Eteobalea serratella* in peppermint (*Mentha piperita*). *Weed Sci.* **47**: 226–232
- Wagner DL, Peacock JW, Carter JL, Talley SE** (1996) Field assessment of *Bacillus thuringiensis* on nontarget lepidoptera. *Environ. Entomol.* **25**: 1444–1454
- Wolfenbarger LL, Phifer PR** (2000) The ecological risks and benefits of genetically engineered plants. *Science* **290**: 2088
- Zangerl AR, McKenna D, Wraight CL, Carroll M, Ficarello P, Warner R, Berenbaum MR** (2001) Effects of exposure to event 176 *Bacillus thuringiensis* corn pollen on monarch and black swallowtail caterpillars under field conditions. *Proc. Natl. Acad. Sci. USA* **98**: 11908–11912

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