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Review

Effects of pollutants on bottom-up and top-down processes in insect–plant interactions

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Pollutants can affect insect herbivores through bottom-up and, possibly, top-down processes.

Abstract

Bottom-up (host plant quality) and top-down (natural enemies) forces both influence the fitness and population dynamics of herbivores. However, the impact of pollutants acting on these forces has not been examined, which prompted us to review the literature to test hypotheses regarding this area of research. A comprehensive literature search found 126 references which examined fitness components and population dynamics of 203 insect herbivores. One hundred and fifty-three of the 203 herbivores (75.4%) had fitness impacted due to bottom-up factors in polluted environments. In contrast, only 20 of the 203 (9.9%) had fitness significantly impacted due to top-down factors in polluted environments. The paucity of results for top-down factors impacting fitness does not necessarily mean that top–down factors are less important, but rather that fewer studies include natural enemies. We provide a synthesis of available data by pollution type and herbivore guild, and suggest future research to address this issue.

Keywords: Pollutants; Bottom-up; Top-down; Herbivores; Performance

1. Introduction

Problems with pollution are substantial, global in distribution, and unfortunately not new (Trumble and Vickerman, 2003). Our planet is becoming increasingly polluted with inorganic and organic pollutants, primarily as a result of human activities (Pilon-Smits and Freeman, 2006). Specific occurrences of anthropogenic pollution can be localized or global and, in either event, pollution can cause changes in insect populations and ecosystems (Heliovaara and Vaisanen, 1993). For the purpose of this review, we will focus on terrestrial ecosystems and the pollutants that are most pertinent to these systems. Contaminants that affect plants and insects in terrestrial ecosystems include air pollutants such as ozone, sulfur oxides (SO_x), nitrogen oxides (NO_x), carbon oxides (CO_x), fluorides and acidic precipitation (acidic fogs and acidic rains), and soil pollutants such as metalloids and heavy metals. These atmospheric and soil pollutants are released into the environment mostly through human endeavors including industry, mining, motorized traffic, agriculture, and military activities.

While common community-level changes observed with the onset of pollution include alterations in species composition as well as reductions in species richness and evenness (Rosenberg and Resh, 2003), there is little information regarding the relative strength of top-down and bottom-up processes in polluted terrestrial ecosystems. Populations of herbivorous insects can be affected by both top-down (natural enemies) and bottom-up (host plant) forces (Hunter and Price, 1992). Pollution-induced environmental changes have effects on plants, herbivores, and natural enemies, thus disrupting tritrophic interactions (for reviews see: Alstad et al., 1982; Reimer and Whittaker, 1989; Heliovaara and Vaisanen, 1993; Fluckiger et al., 2002). Not surprisingly, pollution can disturb the interactions between trophic levels, which results in changes

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in herbivore population density and dynamics through effects on fitness of the herbivore (Zvereva and Kozlov, 2006).

An examination of the literature reporting the effects of pollutants on the fitness of insect herbivores provides insight into the widely variable impact of contaminants on biological systems. In some ecosystems, herbivore fitness is increased in polluted environments, while in others the opposite is evident (see Tables 1 and 2). In still other systems researchers have not detected any effect of pollutants on fitness. Hypotheses regarding pollutant effects on insect herbivores predict that pollutants: (1) induce changes in habitat quality for the herbivore; (2) may modify plant quality; or (3) affect the fitness of natural enemies such that they are reduced or eliminated (Zvereva and Kozlov, 2006). The purpose of this review is to analyze the published literature to test the relative importance of top-down versus bottom-up forces affecting herbivorous insects in polluted environments.

2. Materials and methods

The importance of top-down versus bottom−up forces were examined by determining the numerical responses in the literature to two falsifiable null hypotheses (Table 1). In the first null hypothesis (H_{o1}), the fitness, or population density, of a herbivorous insect due to bottom-up factors in a polluted environment is equal to the fitness, or population density, of a herbivorous insect due to bottom-up factors in a non-polluted environment. The alternative hypotheses ($H_{a1.1}$ and $H_{a1.2}$) provide that bottom-up forces are acting differentially on the fitness, or population density, of an insect herbivore in polluted vs. non-polluted environments: in $H_{a1.1}$ the fitness, or population density, of an insect herbivore is reduced when pollutants are present; in $H_{a1.2}$ the fitness, or population density, is improved when pollutants are present. In the second null hypothesis (H_{o2}), the fitness, or population density, of a herbivore due to top-down factors in a polluted environment is equal to the fitness, or population density, of a herbivore due to top-down factors in a non-polluted environment. The alternative hypotheses ($H_{a2.1}$ and $H_{a2.2}$) provide that top-down forces are acting differentially on the fitness, or population density, of herbivores: in $Ha_{2.1}$ the fitness, or population density, of herbivores is reduced when pollutants are present; in $H_{a2.2}$ the fitness, or population density, is improved when pollutants are present.

The peer-reviewed literature was surveyed to test the hypotheses mentioned previously. References were searched using the University of California's Melvyl System, Web of Science, and AGRICOLA data bases from 1971 to 2007. The literature included both laboratory and field studies. Each study had to meet three criteria for inclusion in this review: (1) herbivore diets (mostly plants, in some cases artificial diet with a level of pollutant that was at an ecologically relevant level for the system being studied) had to compare polluted food sources with an uncontaminated control; (2) at least one aspect of fitness, such as mean relative growth rate (MRGR), development time, weight, fecundity or survival, or (to be inclusive) population density in the field, had to be measured; and (3) studies had to include evidence that bottom-up (host quality) or top-down (natural enemies) processes were assessed. While we are aware that there may be direct effects of pollutants on insect herbivores in terrestrial systems, we could find no reports that pollutants directly act on herbivore fitness. However, there is considerable evidence that pollutants do not directly affect herbivore fitness (Dohmen et al., 1984; McNeill et al., 1987; Trumble et al., 1991; Brown et al., 1992; Redak et al., 1995; Coviella and Trumble, 1999). Thus, for the sake of this review, we assume that the fitness of the insect herbivore is more likely to be affected by indirect (i.e., bottom-up and top-down) processes.

Table 2
Summary of support for hypotheses (see Table 1): results of testing bottom-up versus top-down factors influencing herbivore fitness in polluted environments

Pollutant type	Bottom-up				Top-down			
	Ho1	Ha1.1	Ha1.2	Not tested	Ho2	Ha2.1	Ha2.2	Not tested
SO_2 ($n = 24$)	2	1	21	0	1	0	0	23
NO_2 ($n = 8$)	0	1	7	0	0	0	0	8
CO_2 ($n = 52$)	16	31	5	0	7	4	2	39
Ozone ($n = 18$)	6	3	9	0	2	1	0	15
Acidic precipitation ($n = 14$)	4	1	8	1	0	2	1	11
Heavy metals (n=25)	7	18	0	0	1	1	1	22
Metalloids ($n = 8$)	2	6	0	0	0	0	1	7
Fluoride ($n = 7$)	1	5	1	0	0	0	0	7
Mixtures								
Gases ($n = 9$)	1	0	8	0	3	0	0	6
Ozone, CO_2 (n= 6)	2	1	3	0	1	2	0	3
Gases, heavy metals ($n = 2$)	2	0	0	0	2	0	0	0
Ozone, acidic precipitation ($n = 2$)	0	1	1	0	0	0	0	2
SO_x, heavy metals ($n = 26$)	3	14	6	3	5	2	3	16
Heavy metals ($n = 1$)	0	1	0	0	0	0	0	1
Heavy metals, PCBs ($n = 1$)	0	1	0	0	0	0	0	1
Total ($n = 203$)	46	84	69	4	22	12	8	161

3. Results

One hundred and twenty-six publications were identified which met the criteria for inclusion. These studies included 203 herbivores (Table 2). One hundred and fifty-three of the 203 herbivores examined (75.4%) had fitness, or population density, impacted due to bottom-up factors in polluted environments (Table 2). In contrast, only 20 of the 203 (9.9%) had fitness, or population density, impacted due to top-down factors in polluted environments (Table 2). In examining

Table 1
Falsifiable and alternative hypotheses for predicted effects of pollutants on the fitness of herbivores

Falsifiable hypotheses (Ho)	Alternative 1	Alternative 2
Ho1: The fitness of a herbivore due to bottom-up factors in a polluted environment = the fitness of a herbivore due to bottom-up factors in a non-polluted environment	Ha1.1: The fitness of a herbivore due to bottom-up factors in a polluted environment < the fitness of a herbivore due to bottom-up factors in a non-polluted environment	Ha1.2: The fitness of a herbivore due to bottom-up factors in a polluted environment > the fitness of a herbivore due to bottom-up factors in a non-polluted environment
Ho2: The fitness of a herbivore due to top-down factors in a polluted environment = the fitness of a herbivore due to top-down factors in a non-polluted environment	Ha2.1: The fitness of a herbivore due to top-down factors in a polluted environment < the fitness of a herbivore due to top-down factors in a non-polluted environment	Ha2.2: The fitness of a herbivore due to top-down factors in a polluted environment > the fitness of a herbivore due to top-down factors in a non-polluted environment

fitness and population density impacts by pollutants, the following positive and negative patterns emerged for bottom-up and top-down processes.

3.1. Bottom-up effects

For bottom-up processes, positive effects on fitness were observed for insects (see Supplementary material, Addendum Table for references) due to changes in plant quality. Plants exposed to air pollutants frequently become better hosts for herbivores. Aphids on host plants fumigated with SO_2, NO_2, or ozone generally exhibited significant increases in the mean relative growth rate (MRGR), which subsequently led to population increases (Dohmen et al., 1984; McNeill et al., 1987; Warrington, 1987, 1989; Warrington et al., 1987; Dohmen, 1988; Houlden et al., 1990; Summers et al., 1994). The effects of SO_2 or ozone fumigations on *Epilachna varivestis* Mulsant also resulted in significantly faster growth, as well as increased size and fecundity (Hughes et al., 1981, 1982, 1983, 1985a; Chappelka et al., 1988; Lee et al., 1988). When host plants were exposed to ozone, the aphid species *Diuraphis noxia* (Kurdjumov) and *Rhopalosiphum padi* (Linnaeus), and the Lepidopterans *Keiferia lycopersicella* (Walshingham) and *Malacosoma disstria* Hubner displayed increases in fitness through increased MRGR, weight gain, faster development, and survival (Trumble et al., 1987; Warrington, 1989; Summers et al., 1994; Percy et al., 2002; Holton et al., 2003; Kopper and Lindroth, 2003b). In the field, the aphid species, *Chaitophorus stevensis* Sanborn, exhibited significantly higher population peaks when exposed to elevated ozone levels (Percy et al., 2002). Mixtures of various gases have produced a positive effect on fitness of herbivores, most notably increases in the population growth rate of aphids (Braun and Fluckiger, 1985; Dohmen, 1985; Bolsinger and Fluckiger, 1987; McNeill et al., 1987; Holopainen et al., 1991, 1993). Mixtures of some pollutants such as the combination of SO_x and heavy metals can sometimes allow herbivores in moderately polluted habitats to increase population densities (Zvereva et al., 1995a; Kozlov, 2003); however, the reason for this is often unclear. Most studies suggest that air pollutants impact the host plants such that additional nutrients (often amino acids, proteins or carbohydrates) are available to the insects (Reimer and Whittaker, 1989; Trumble et al., 1993; Fluckiger et al., 2002).

Probably the most investigated air pollutant is CO_2. Four orders of insects in 14 families (Addendum Table) have been studied. Only a small subset of aphids appeared to benefit from exposure of their host plants to elevated CO_2 (Bezemer et al., 1998, 1999; Stacey and Fellowes, 2002). The species *Brevicoryne brassicae* (Linnaeus) (Stacey and Fellowes, 2002), *C. stevensis* (Percy et al., 2002) and *Myzus persicae* (Sulzer) (Bezemer et al., 1998, 1999) exhibited responses which included faster population growth rates, increased fecundity and higher population peaks. Other aphid species showed no significant effects (Docherty et al., 1997; Bezemer et al., 1999; Stacey and Fellowes, 2002; Awmack et al., 2004). Thus, a substantial majority of insects did not gain a fitness benefit from exposure of their hosts to elevated atmospheric CO_2 (Butler et al., 1986; Johnson and Lincoln, 1990; Lindroth et al., 1993; Williams et al., 1994; Kinney et al., 1997; Kopper et al., 2001; Kopper and Lindroth, 2003b).

Acidic precipitation, in general, also can increase the fitness of herbivores through bottom-up processes (Table 2). Noctuids gained significantly more weight and showed increased rates of development on plants exposed to acidic precipitation (Stinner et al., 1988; Trumble and Hare, 1989). Aphids exhibited increases in MRGR and increases in fecundity, while chrysomelids displayed mixed responses in terms of fitness effects (Neuvonen and Lindgren, 1987; Hall et al., 1988; Kidd, 1990; Palokangas et al., 1995; Redak et al., 1997). Some of the fitness improvements were related to physiological responses to physical damage caused by acidic precipitation, while increased nitrogen deposition was credited for improved survival and development in other systems (Stinner et al., 1988; Trumble and Hare, 1989).

Regardless of the beneficial effects just described, the majority of research has indicated that pollutants reduce host plant quality, resulting in bottom-up effects with negative consequences for herbivore fitness (Table 2). For example, following ozone exposure to their host plants, chrysomelids had decreased fitness (Coleman and Jones, 1988a; Jones and Coleman, 1988). The most common detrimental response to ozone was a decrease in fecundity (Coleman and Jones, 1988a). In some cases, behavioral effects were observed, including an avoidance of ozonated foliage for oviposition (Jones and Coleman, 1988). Another effect of elevated ozone levels was a reduction in colonization rates by the leafminer, *Phyllonorycter tremuloidiella* (Braun) (Kopper and Lindroth, 2003a). Lepidoptera were negatively affected by increased atmospheric CO_2. Reduced fitness was evidenced by significant decreases in growth, survival, development, and size of larvae and adults (Lincoln et al., 1986; Osbrink et al., 1987; Akey and Kimball, 1989; Fajer et al., 1989; Lindroth et al., 1993, 1995, 1997; Roth and Lindroth, 1994; Traw et al., 1996; Buse et al., 1998; Lindroth and Kinney, 1998; Roth et al., 1998; McDonald et al., 1999; Stiling et al., 1999; Agrell et al., 2000; Coviella and Trumble, 2000; Coviella et al., 2000; Johns and Hughes, 2002; Percy et al., 2002; Holton et al., 2003). A similar result was obtained for one species of grasshopper, *Melanoplus sanguinipes* (Fabricius), which exhibited significant decreases in growth (Johnson and Lincoln, 1990).

Heavy metals reveal a pattern of primarily negative effects on fitness for herbivores. Studies that included 16 families of insects over five orders reported reductions in weight, growth, survival, fecundity, and eclosion success (Sell and Bodznick, 1971; Haney and Lipsey, 1973; Sivapalan and Gnanapragasam, 1980; Schmidt et al., 1991; Gintenreiter et al., 1993; Boyd and Martens, 1999; Kazimirova et al., 1997; Boyd and Moar, 1999; Kramarz and Stark, 2003; Behmer et al., 2005; Coleman et al., 2005; Jhee et al., 2005, 2006b; Scheirs et al., 2006; Goncalves et al., 2007; Noret et al., 2007; van Ooik et al., 2007). A similar pattern was found for metalloids, most notably selenium (Se): exposure to Se-contaminated plants significantly decreased growth, larval weight, and survival of *Spodoptera exigua*

(Hubner), *Pieris rapae* (L.), and *Plutella xylostella* (L.) (Trumble et al., 1998; Vickerman et al., 2002; Hanson et al., 2003; Freeman et al., 2006). With fluoride, the few studies available suggested a trend of decreasing fitness of herbivores. For example, *Bombyx mori* (L.), typically displayed decreased growth and feeding rates when fed fluoride-polluted foliage (Alstad et al., 1982 and references therein). A comparable response was observed for *E. varivestis*, *Tribolium confusum* (duVal), noctuids and lymantrids (Johansson and Johansson, 1972; Weinstein et al., 1973; Hughes et al., 1985b; Mitterbock and Fuhrer, 1988).

Publications describing the effects of mixtures of pollutants are not common. However, a negative effect on fitness typically occurred when mixtures contained heavy metal particulates (Heliovaara et al., 1982, 1989a,b; Heliovaara and Vaisanen, 1989; Koricheva and Haukioja, 1992; Koricheva, 1994; Zvereva et al., 1995b; Ruohomaki et al., 1996; Kozlov et al., 2000; Jhee et al., 2006a; Culliney and Pimentel, 1986). Herbivores exhibited declines in fitness by significant decreases in survival, longevity, fecundity, size, and increases in developmental times.

3.2. Top-down effects

Only 20 cases of the 203 herbivores examined (9.9%) had fitness, or population density, impacted by top-down processes in polluted environments (Table 2). Perhaps the most notable observation was the number of studies (161, 79.3%) that did not examine higher trophic levels. This is likely due to the increased difficulty and complexity in designing experiments with multiple trophic levels. Not surprisingly, some pollutants, such as NO_2 and fluoride, have not been examined for top-down factors influencing herbivore fitness. In addition, there are few studies that have examined the effects of mixtures of pollutants on top-down factors that affect herbivore fitness (Heliovaara et al., 1982, 1991; Zvereva and Kozlov, 2000; Percy et al., 2002; Holton et al., 2003; Awmack et al., 2004; Zvereva and Kozlov, 2006). Thus, many opportunities still exist for research in multitrophic systems in the laboratory and the field.

The relatively few studies published that examine pollution effects on insect parasitoids, predators, and pathogens do provide evidence of possible trends. For example, in environments exposed to elevated CO_2, the most common responses were either no effect or negative effects on the fitness of herbivores due to top-down processes (Lindroth et al., 1997; Bezemer et al., 1998; Stiling et al., 1999; Coviella and Trumble, 2000; Stacey and Fellowes, 2002; Holton et al., 2003; Kopper and Lindroth, 2003b; Awmack et al., 2004). We initially anticipated that the slowed growth of some herbivorous larvae would increase the opportunity for upper trophic level control. However, no reports were found to support this possibility: percent parasitism or numbers of prey eaten by predators did not change in polluted environments (Stacey and Fellowes, 2002; Bezemer et al., 1998). One study suggested parasitism might be positively affected. Stiling et al. (1999) found increasing mortality in leafminers from parasitoids in environments exposed to elevated CO_2. They offered two mechanisms to explain the increased death rates of leafminer in their study: (1) the direct effect of reduced leaf quality (lower N and elevated C/N); and (2) an indirect trophic cascade, such as: (a) larger miners are easier for parasitoids to find because of more feeding by leafminers to gain necessary nitrogen from plants; (b) delayed growth may have prolonged exposure to parasitoids; or (c) larvae were weakened and more susceptible to parasitoid attack. Awmack et al. (1997) and Mondor et al. (2004) did demonstrate that elevated CO_2 conditions caused the aphid species, *Aulacorthum solani* (Kaltenbach) and *C. stevensis*, to lose the ability to detect alarm pheromones, suggesting the aphids were at greater risk for mortality by predators and parasitoids. Conversely, aphids exposed to elevated ozone exhibited greater sensitivity to alarm pheromones, which augmented escape responses (Mondor et al., 2004). However, there were no empirical data presented in either study for predation or parasitism of aphids to support the speculation. However, in another case, elevated CO_2 and ozone levels demonstrated a disrupted synchrony between natural enemies and aphid hosts, thus long-term regulation of aphid populations may be less effective under elevated air pollution levels (Percy et al., 2002). In a study by Palokangas et al. (1995) examining the effects of a chrysomelid beetle feeding on foliage exposed to acidic precipitation, the fitness of *Phratora polaris* (Schneider) decreased because the larvae were more susceptible to natural enemies. The mechanism for increased vulnerability to predators is unclear, but the authors speculate the mechanism may be related to a decrease in defensive compounds in the beetles (Palokangas et al., 1995).

In a study with heavy metals by Kramarz and Stark (2003), the instantaneous growth rate for the aphid *Acyrthosiphum pisum* (Harris) was decreased significantly by 20%, but the instantaneous growth rate was decreased by 40% for the parasitoid, *Aphidius ervi* Haliday. Heavy metals and metalloids such as Se can also increase the encapsulation rate of parasitoids and offer protection for herbivores from viruses and bacteria, probably as a result of increased immune responses (Popham et al., 2005; van Ooik et al., 2007). Vickerman and Trumble (2003) reported that the generalist heteropteran predator, *Podisus maculaventris* Say, reared on host larvae fed diets containing sodium selenate took longer to develop, had significantly higher mortality, and weighed less than controls. The overall impact was speculated to result in a substantially negative outlook for the predator population. Mixtures of gases containing heavy metal particulates show effects of increasing fitness for herbivores by detrimentally acting on top-down influences (Heliovaara et al., 1991; Zvereva and Kozlov, 2000, 2006). In the field, significant reductions have been observed for mortality caused by parasitism and virus infection of herbivores in polluted environments (Heliovaara et al., 1982, 1991).

The impacts of pollutants on the effectiveness of insect pathogens have shown mixed results. In a study by Trumble et al. (1991), the efficacy of *Bacillus thuringiensis* was not affected by acidic precipitation. However, acidic precipitation was shown to reduce the *Neodiprion sertifer* nuclear polyhedrosis virus (NsNPV) transmission efficiency to first instar

Neodiprion sertifer (Geoff.) (Saikkonen and Neuvonen, 1993). While in another case, the susceptibility of *Lymantria dispar* (Linnaeus) to nuclear polyhedrosis virus (NPV) was not affected in elevated CO_2 treatments (Lindroth et al., 1997). Interestingly, elevated atmospheric CO_2 led to increased feeding by *S. exigua*, resulting in increased toxicity of foliar applications of *B. thuringiensis* (Coviella and Trumble, 2000).

3.3. Guild effects

We have also found guild effects (Fig. 1). Insects that are foliage feeders or miners often exhibit detrimental impacts of pollutants through bottom-up process in CO_2 and heavy metal polluted environments. This includes mixtures that contain heavy metal particulates. Also interesting are phloem feeders that exhibit greater fitness in environments polluted by SO_2 and NO_2 or a combination of these gases. There are few cases of pollution effects on bottom-up or top-down processes on xylem feeders, mesophyll feeders, seed feeders, and gallers, however not enough to determine a definite pattern. There is practically no information on pollution effects of bottom-up or top-down processes on the fitness of borers, root feeders and pollinators.

4. Discussion

Pollutants can alter tritrophic interaction, and a review of the literature has illustrated that these alterations can be

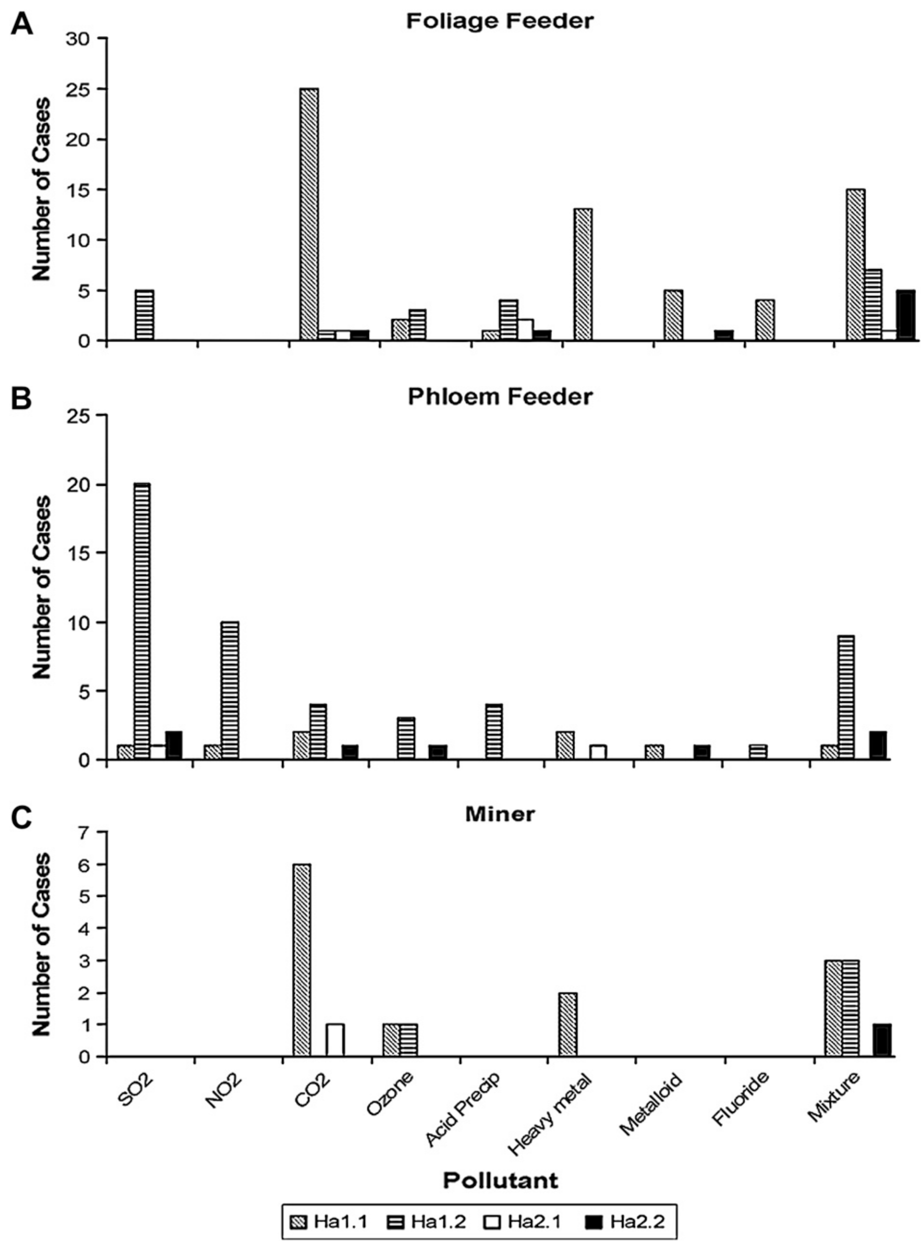

Fig. 1. Summary of support for hypotheses (see Table 1): results of negative and positive bottom-up versus top-down effects of pollutants on herbivore fitness by feeding guild. (Null hypotheses were not included due to relatively few examples.)

accomplished through both bottom-up and top-down processes. For bottom-up processes, pollutants clearly can affect the quality of a plant, changing either the nutritional status or toxicity for the herbivore. Positive bottom-up effects on fitness of herbivores in polluted environments are relatively common. In particular, air pollutants can enhance the release of soluble nitrogen and sugars, which can have strong effects on an insect herbivore such as increased phagostimulation, growth, and reproduction (Fluckiger et al., 2002). However, heavy metal particulates which land on plant surfaces can damage photosynthetic systems and result in more toxic plant chemistries with decreased nutritional value (Jensen and Trumble, 2003). For plants grown in elevated CO_2 environments, increased carbon to nitrogen ratios may modify the within-plant distribution and availability of nitrogen, and along with increases in carbon-based defenses cause a loss in fitness to herbivores (Coviella and Trumble, 1999).

Similarly for top-down processes, pollutants can have multiple effects. Detrimental impacts on fitness occur if the herbivore is weakened by poor host plants and becomes more susceptible to attack. However, some higher trophic level organisms show a relatively greater loss of fitness relative to the herbivore. This occurs if the pollutant is more toxic to the higher trophic levels, or if the immune system of the herbivore is elevated by the exposure to pollutants. Predicting the likely effects of pollution exposure is hampered by the paucity of available top-down studies.

This review has identified a number of research areas that need to be addressed before any reliable predictions can be made for pollution exposure. Foremost is the scarcity of studies of top-down forces, in comparison to bottom-up forces, that have examined the fitness of herbivores in polluted environments. Specifically, no research is available on the impacts of NO_2 and fluoride on top-down factors influencing herbivore fitness. Relatively few studies have examined the impacts of pollution on parasitoids, predators, and pathogens in relation to fitness effects on herbivores.

Because of the complexity and variability of pollutants, plants and herbivores in field systems, most studies (ca. 68% of included studies examined) have been conducted in the laboratory where environmental factors can be carefully controlled. However, at some point more research must be moved into the field in order to validate the laboratory studies. A few studies do combine approaches of laboratory and field-based experiments (i.e., McNeill et al., 1987; Trumble et al., 1987; Saikkonen et al., 1995; Zvereva et al., 1995a,b; Kozlov et al., 1996). In addition, comparisons of diverse systems such as prairie or desert ecosystems, and even urban environments, are needed to improve our understanding of ecosystem factors that influence which mechanistic responses to pollutants will be dominant.

More research is also needed on a wider diversity of plants and arthropod herbivores. Approximately 48% of the host plants used in experiments from the referenced data set were trees while the next largest category was agricultural crops (ca. 30%). Furthermore, an additional 9% of the studies focused on pollutants in artificial diets. Thus, less than 13% of the research has focused on native systems, which have the greatest diversity of plants and herbivores. Similarly, more diverse families of herbivorous insects could be investigated. By far the most studied family in the data set was aphids, which comprised 23% of the case studies. The next most studied group of herbivores was the noctuids and lymantriids, which made up 22% of the case studies. Thus, just three families of insects accounted for over 45% of the test organisms. Undoubtedly these herbivore groups were chosen because of their economic importance and ease of rearing. Also, two orders of insects are only represented by a single family. For example, the Orthoptera, which are >99% phytophagous, are only represented by a single family (Acrididae) and the phytophagous Hymenoptera are only represented by the family Diprionidae. Similarly there are few studies that have examined phytophagous Diptera and the only two families represented are the Tephritidae and Agromyzidae. Virtually no studies have been conducted on the fitness effects of pollutants on other orders of phytophagous insects. Thus, given the remarkable diversity of arthropod herbivores, the opportunities to expand data collection to include novel families, or even guilds of herbivores, are exceptional.

There is also a substantial need for more thorough research on herbivore fitness correlates. A majority of studies we found only measured one or two fitness components of the immature stage. Measurements typically included the development or growth rate and survival of immatures. The exception was reproduction, which was measured in approximately 36% of the studies we examined. A wide range of additional sublethal effects can be tested, including changes in lifespan, fertility, sex ratio, and modifications in such critical behaviors as feeding, host acquisition, and ovipositon (Jensen and Trumble, 2003). Likewise, approximately 37% of the case studies examined did observe the effects of pollutants on behaviors (i.e., feeding and oviposition preferences, and defensive behaviors), and a few studies have examined pollutant effects on behaviors specifically, however without measuring the effects of pollutants on fitness correlates (Agrell et al., 2005; Awmack et al., 1997; Jhee et al., 1999; Jiang et al., 2005; Mondor et al., 2004; Paine et al., 1993; Pollard and Baker, 1997; Vickerman and Trumble, 1999).

Lastly, additional research is needed on mixtures of pollutants, and in particular, industrial compounds. Approximately 29% of the case studies examined mixtures of pollutants. In nature, pollutants rarely occur in isolation. Unfortunately, due to the complexities of testing multiple pollutants, the interactions of contaminants are poorly understood (Cain et al., 2000). A significant number of toxic chemicals have been released in large quantities intentionally or accidentally from industrial sources (e.g., polychlorinated biphenyl congeners and dioxins), but less attention has been paid to the effects of these compounds on arthropods (Heliovaara and Vaisanen, 1993). Overall, research on the role of mixtures of pollutants in modifying tritrophic interactions will probably be more meaningful than studies of individual chemicals. Information that documents when one process becomes relatively more important than another will allow improved prediction of the impacts of pollution at the bottom of the food web in a rapidly changing environment.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.envpol.2007.12.026.

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