

## *Species Interactions*

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### ABSTRACT

Effects of pollutant mixtures on interactions between species (symbiosis, predation, herbivory, parasitism, and competition) and methods for measuring those effects are critically reviewed. While numerous field studies have shown that responses to pollutants are mediated or modified by species interactions, the relative importance of direct effects on survival and growth of the individual participants versus effects on the rate of interaction is unclear. The sensitivity of species interactions in the laboratory suggests their use in screening tests but the expense and complexity of such systems have discouraged such use. Use of species interaction tests to predict the type and level of effects is hampered by the large number of interactions and our inability to extrapolate test results between pairs of interacting species. In the near term, species interaction tests are most likely to be useful in predicting effects on simple systems with only a few interactions such as crops, pastures, and monospecific forests. In the long term, greater use of species interaction tests will depend on evidence from field studies that assessments based on single species tests are failing due to lack of knowledge about species interactions.

### 1 INTRODUCTION

The phrase 'species interactions' covers most of the domain of ecology. The subject is bounded on one side by autecology, the study of the responses of organisms of a single species to their environment including toxicants, and on the other by ecosystems ecology, the study of whole biogeochemical systems. These boundaries are somewhat hazy; tight symbiotic relationships may respond like a single organism and a set of trophic relationships can constitute the bulk of an ecosystem's dynamics. I will limit this discussion for the sake of consistency to interactions of pairs of species.

In this paper I will illustrate and discuss the following conclusions: (1) species interactions have been studied in numerous laboratory systems that might be adapted for toxicity testing; (2) species interactions could significantly alter toxicant effects, and vice versa; (3) effects of toxicants on species interactions (as

opposed to direct toxicant-induced effects on the population size of one species which subsequently affects other species through trophic or competitive interactions) have received limited attention in field studies; (4) laboratory studies of toxicants and species interactions are rare relative to other types of toxicological studies; (5) a few species interactions could be readily and beneficially included in hazard assessments; and (6) there is no pressing need for the development of additional tests of species interactions until we better understand the role of species interactions in toxicological responses in the field.

The current dearth of tests for species interactions is not primarily due to a lack of laboratory systems that could be adapted to toxicology. Considerable effort by ecologists and pathologists has been devoted to the study of this subject in the laboratory. Because laboratory multispecies systems have recently been reviewed at length with respect to their practicality as test systems (Giddings, 1981; Suter, 1981a), I will not repeat that review here. Rather, I will present a summary of the available evidence concerning the significance of interplay between toxicants and species interactions and discuss the potential role of species interaction test systems in toxicity assessment.

## 2 SPECIES INTERACTIONS AND CHEMICAL MIXTURES

This review is organized in terms of the standard categories of species interactions (symbiosis, predation, herbivory, parasitism, and competition), but this organization is primarily a convenience. These categories of interactions have no toxicological consistency. For example, the responses to toxicants of two flour beetle species in a jar of flour are not representative of competition in general in the sense that white mice are representative of mammals in general. While white mice share most physiological and morphological features in common with other mammals, the egg predation that is so important in competition between flour beetles (Mertz, 1972) does not occur in most other competitive relationships. Because species interactions are categorized on the basis of their outcome rather than their mode of action, chemicals could not be expected to affect all members of a class of interactions in the same way.

While the subject of this volume is mixtures of chemicals, species interactions have not been used to test the interactive effects of combinations of chemicals. I will address the theme by, as far as possible, drawing my examples from studies of complex pollutants such as oils and ambient air pollution. The examples are drawn primarily from the literature on the effects of air pollutants on plants. There is a relatively large body of data on the effects of air pollution on the interactions of plants with other species because the exposed and sedentary nature of plants makes them easy to monitor in the field. Aquatic studies and other literature will be used in a supporting role but they are primarily based on laboratory studies so their relevance to the field is less certain.



## 2.1 Parasitism

The relationship between a host and parasite (including microbial parasites) may be affected by pollutants and the response of a host to pollutants may be affected by the presence of parasites. Most susceptibility to parasites can be affected by pollutant-induced changes in physiology, surface chemistry, internal fluid chemistry, injuries which provide routes of entry, general weakening of the host, or even effects on symbionts such as mycorrhizae and 'cleaner' organisms which suppress parasites. In addition, the virulence of a parasite may be affected by the direct stimulatory or toxic effects of pollutants. Finally, the host-parasite relationship may affect responses to pollutants by weakening either species, changing their physiology, or changing the rate of pollutant uptake. In the real world, these mechanisms interact to produce complex causal relationships.

The interactions between air pollution, plants, and plant parasites have drawn considerable attention resulting in five recent reviews (Heagle, 1973; Manning, 1975; Smith, 1981; Treshow, 1975, 1980). Pollutants more often suppress rather than promote parasitism (Treshow, 1975), but promotion is not uncommon. Studies of the effects of parasitism on biotic responses to air pollution also give mixed results but a variety of parasites appear to reduce oxidant injury of host plants (Davis and Smith, 1975; Heagle, 1973; Moyer and Smith, 1975).

Recently, considerable interest has centred on interactions between air pollutants, trees, and root-rot fungi. This interest has been stimulated by studies in southern California where *Fomes annosus* has been implicated in the increased mortality of oxidant-exposed ponderosa and Jeffrey pine (Kickert *et al.*, 1980; Miller *et al.*, 1977). *Fomes innoculum* spread more rapidly in cut stumps of severely oxidant-injured pines than slightly injured or uninjured pines (James *et al.*, 1980). Similarly, Skelly (1980) found in Virginia that dying white pines with severe oxidant injury symptoms also had roots infected by the fungus, *Verticicladiella procera*. These results suggest that attacks on woody tissues by fungi are promoted by air pollution. However, studies at industrial facilities in Montana (Scheffer and Hedgcock, 1955), Poland (Grzywacz and Wazny, 1973), and Czechoslovakia (Jancarik, 1961) indicate that a particular emission may either promote or inhibit fungal parasitism of woody tissues depending on the host and parasite species.

A few researchers have examined host-parasite-toxicant interactions in aquatic systems. Reviews by Wedemeyer (1970) and Snieszko (1974) indicate that stress, including exposure to toxicants, increases the susceptibility of fish to parasites. Most of the instances from the field involve a circumstantial association between high pollution levels and mass mortalities of bacteria-infected fish. Experimental studies reveal instances of both increased and decreased infection of fish and aquatic invertebrates by microbial parasites in the presence of pesticides (Snieszko, 1974). Parasites may also affect the susceptibility of their hosts to toxic materials. For example, parasitic freshwater

mussel glochidia increased the sensitivity of coho salmon fry to toluene, naphthalene, and a water-soluble fraction of crude oil (Moles, 1980) and cestode parasitized sockeye salmon smolts were more sensitive to zinc than healthy smolts (Boyce and Yamada, 1977).

## 2.2 Herbivory

Like host-parasite relationships, plant-herbivore interactions may be affected by pollutant interplay with the physiology and physical condition of either participant. Air pollution-plant-herbivore interactions have been reviewed by Heagle (1973), Smith (1981), and Alstad *et al.* (1982). Insect herbivory has been observed to be either promoted or inhibited depending on the species, pollutants, and dose involved. Promotion of herbivory has been observed in the field more often than inhibition, but this generalization may be attributed to the fact that increases in insect damage are more conspicuous than decreases.

Heagle (1973) hypothesized that herbivorous insects would be promoted if they are protected from the pollutants and if they are most successful when attacking weakened plants. This generalization is largely based on observations that bark beetles, which are protected from gaseous pollutants, are often associated with trees damaged by air pollution. Even within this specific class of herbivores, generalization is difficult. Western pine beetles contribute to mortality of oxidant-injured pines but damaged trees appear to suppress brood production thereby reducing the probability of an outbreak involving healthier trees (Kickert *et al.*, 1980). As a further complication, bark beetles may be particularly sensitive to pollutants such as fluorides which accumulate in vascular fluids (Heagle, 1973).

While herbivory on phytoplankton is very difficult to measure in the field, filtration and assimilation rates of herbivores can be measured in the laboratory. Effects of various oils on planktonic herbivory have been studied for larval lobsters (Wells and Sprague, 1976) and clams (Keck *et al.*, 1978), copepods (Berman and Heinle, 1980) and *Daphnia* (Geiger and Buikema, 1981; Ullrich and Milleman, 1983). These studies generally show decreased filtration and assimilation but increases may also occur at low concentrations of oil (Ullrich and Milleman, 1983). Because the algae are essentially passive in these interactions, they can be (and often are) replaced with inert particles.

## 2.3 Predation

Predation is difficult to monitor quantitatively in nature, so evidence suggesting the importance of predation-pollution interactions is meagre. The studies of smog effects on southern California pine forests have found no effects on predators of pine bark beetles (Kickert *et al.*, 1980). Hymenopteran parasitoids of black pine leaf scale are suppressed by dust resulting in increased scale



densities but the effect seems to be due to wasp mortality rather than interference with the species interaction (Alstad *et al.*, 1982; Edmunds, 1973). Reductions in insect predation are frequently observed following pesticide applications but these effects also are generally attributed to predator mortality (DeBach, 1974; Pimentel, 1971). Hence, single species tests would appear to be adequate to predict these effects.

There is a large body of laboratory-derived literature on aquatic predation including many studies of chemical effects (Giddings, 1981). Unfortunately in nearly all of these studies only the prey were exposed to the chemicals so the nature and magnitude of the observed effects cannot be related to the field, where both species are exposed. These studies indicate that decreased avoidance behaviour may occur at very low concentrations of chemicals, but we have no idea whether predation rates are significantly changed in the field by ambient pollutant mixtures. The reported effects of lake acidification on predation are due to loss of predaceous fish rather than a change in the predation process (Eriksson *et al.*, 1980; Yan *et al.*, 1982).

## 2.4 Symbiosis

Symbiotic relationships frequently appear to be sensitive to toxic materials, possibly because the maintenance of mutual benefit requires close physiological regulation. Lichens, which are symbiotic associations of algae and fungi, are extremely sensitive to gaseous air pollutants (Ferry, 1982; Ferry *et al.*, 1973). This sensitivity is well documented by both laboratory and field studies and is generally attributed to breakdown of the relationship rather than simple mortality of either symbiont. The observed reductions in the abundance of lichens at low ambient pollutant concentrations may be due to shifts in the metabolic balance between the partners (Nieboer *et al.*, 1976).

Mycorrhizae, the symbiotic association of fungi with the roots of higher plants, may be sensitive to pollutants that accumulate in plants or the soil. Sobatka (1964) and Grzywacz (1964) found declines in mycorrhizal associations with tree roots near industrial pollution sources. Field fumigations of Montana grasslands with sulphur dioxide resulted in decreased mycorrhizal infection of western wheatgrass (*Agropyron smithii*) and changes in the mycorrhizal structure at concentrations of sulphur dioxide that did not affect above-ground biomass (Rice *et al.*, 1980). Laboratory studies have shown effects on mycorrhizae due to sulphur dioxide and nitrogen dioxide (Garrett, 1978), ozone (McCool *et al.*, 1979), and pesticides (Menge *et al.*, 1979).

Because of the economic importance of leguminous crops, the response of the legume-rhizobium symbiosis to a variety of gaseous pollutants, metals, and agricultural chemicals has been tested (Garten, 1985; Suter, 1981a). Although the significance of these responses has not been determined in the field, the fact that *in vitro* responses of rhizobia are poorly correlated with growth and yield of the

whole microbe–plant systems suggests that the interaction itself may need to be tested.

Studies of the effects of pollutants on aquatic symbiotic relationships could not be found during Giddings' (1981) literature review. He concluded that symbiosis is relatively unimportant in aquatic systems with the exception of the symbiosis of zooxanthellae and coral polyps.

## 2.5 Competition

Competition is probably the least studied class of species interactions with respect to pollution effects. Smog in southern California appears to be causing competitive replacement of sensitive ponderosa and Jeffrey pine by less sensitive trees and shrubs (Miller, 1973) but the process is slow and the mechanisms are ill-defined. Oxidant air pollution has been implicated in the competitive decline of clover in pastures planted to clover and grass (Blum *et al.*, 1980; Kochar *et al.*, 1982). Laboratory studies indicate that the effects of ozone on clover–grass competition depend on the species used, the presence of parasites, and the specifics of treatment (Bennett and Runeckles, 1977; Kochar *et al.*, 1980, 1982). Ozone may even induce an allelopathic effect of fescue (*Festuca arundinacea*) on white clover (*Trifolium repens*) (Kochar *et al.*, 1980).

Laboratory studies of the effects of aquatic pollutants on competition have been largely confined to algae. Shifts in competitive relationships between algal species can be caused by very low concentrations of chemicals in laboratory studies (Giddings, 1981), but effects in the field are poorly documented. Trace concentrations of  $\text{Cu}^{2+}$  caused shifts in the species composition of a eutrophic lake, presumably due to the competitive disadvantage of blue-green algae following suppression of their nitrogen-fixation capabilities (Horne and Goldman, 1974). Because the shift in phytoplankton species composition in acidified lakes is associated with decreases in phosphorus concentrations, it seems likely that competitive processes are involved (Hendrey, 1982).

## 3 USES OF MULTISPECIES TESTS

Toxicity testing of complex materials can serve three purposes: (1) screening to determine whether a potential exists for toxic effects in the receiving system; (2) prediction to determine whether the toxic effects are likely to be significant; and (3) monitoring to determine the variation in the toxicity of a complex effluent. The utility of species interaction tests for each of these tasks is discussed below.

### 3.1 Screening

Screening is the first level of testing of a complex material or individual chemical. It is intended to eliminate from further consideration those materials that are clearly acceptable at their expected release rate. To serve this purpose, a test should be sensitive, inexpensive, and rapid.

There are at least three reasons why tests using species interactions might be



more sensitive than single species tests. First, the stress of dealing with predators, parasites, or competitors may reduce the resources available to an organism to deal with toxicants. Second, the potential range of responses to toxicants is increased by the presence of interacting species. For example, complex behaviours such as those involved in capturing prey or avoiding capture are often sensitive to toxic effects and are absent from standard, single species tests. Third, successful physiological adaptation to toxicants becomes less probable when a physiological or biochemical co-adaptation with a second species must be maintained.

Tests of interactions among two or three species are also likely to be more sensitive than ecosystem processes involving a diverse community. Ecosystem processes, unlike species composition and abundance, are stabilized by taxonomic diversity (McNaughton, 1977). The major ecosystem processes, fixation and release of energy and minerals, are performed by numerous species which vary in their sensitivity. Therefore, sensitive species which are reduced by toxic stress are often functionally replaced by resistant species. This phenomenon which is called 'congeneric homotaxis' (Hill and Durham, 1978; Hill and Weigert, 1982) tends to buffer ecosystem processes against the effects of toxicants.

Although the sensitivity of species interaction systems suggests that they might be useful in toxicity screening, they are typically more expensive and lengthy than currently used screening tests. Further, the existing screening tests might easily and inexpensively be made more sensitive by using stressful physical and chemical conditions rather than a second organism. In current practice, sensitivity is supplied through the application of safety factors to relatively insensitive screening test results (Cairns *et al.*, 1978). Therefore, multispecies tests are likely to be used for screening only if they can be shown to provide a more accurate screen. An accurate screening test is one that responds at concentrations of chemicals that are linearly related to the safe concentration in the field. Currently, we know very little about the actual safe concentration in the field of either complex materials or single chemicals. Therefore, we cannot define the magnitude of error associated with the relationship between screening test results and field responses. Until we better evaluate the accuracy of existing screening tests, it would be unreasonable to recommend multispecies screening tests.

### 3.2 Prediction

Chemicals or complex materials which do not pass the screening level of testing are assumed to have a potential for affecting the environment. Further testing is applied to these chemicals to predict the effects of the material and assess the acceptability of those effects. The selection of test systems for predictive assessment is predicated on a conceptual model of the system whose response is being predicted.

Clearly, if species interactions and toxic effects interact in important ways, it is inappropriate to limit environmental toxicology to prediction of direct toxic effects. However, because the response of individual organisms to toxic materials

forms the basis for all subsequent effects on species interactions or ecosystem processes, single species responses are a logical starting point for predictive assessment. Techniques exist for extrapolating the toxic responses of individual organisms between species and between types of responses to predict individual responses of untested species or to parameterize models of species interactions (Suter *et al.*, 1983). Forest stand models (Botkin and Aber, 1979; Kercher and Axelrod, 1981; West *et al.*, 1980) and a lake ecosystem model (O'Neill *et al.*, 1982) have been adapted to predict the effects of species interactions on toxic effects. These models generate results that are intuitively appealing, but they have not been validated by comparison with the responses of real ecosystems to toxic materials.

The use of single species responses to parameterize multispecies models relies on the assumption that the dynamics of the species interactions are not affected by the toxicants. For example, in the use of FORET by West *et al.* (1980) to predict air pollution effects on a deciduous forest, pollutants were assumed to affect only the growth rate of the trees. Changes in the nature of the interactive processes, such as the appearance of allelopathic effects under the influence of ozone observed by Kochar *et al.* (1980), are unaccounted for. Also neglected are certain effects of pollutants on individual organisms that are not measured in routine single species tests and which are critical to species interactions. For forests, these might include changes in tolerance of shade, drought, or low nutrient status.

Clearly, if toxic materials frequently affect the dynamics of important species interactions (i.e. if there are emergent properties of the toxicant-species interaction system), single species tests are not adequate to parameterize models of toxic effects. The problem is choosing a limited number of practical tests that adequately represent important species interactions.

The problem of limiting the number of tests is solved by selecting tests to represent categories of entities that are exposed to toxicants. For single species toxicology, these categories are usually taxonomic, for example the albino rat represents all mammals. As explained in the introduction, the conventional categories of species interactions are not toxicologically consistent and no small set of tests could serve to represent them. The idea of tests to represent taxonomically based sets of interactions (e.g. predation by fish on fish) is appealing since it offers consistency in the physiological responses of the component species, but it does not seem to be a sufficient criterion. For example, chemicals which cause hyperactivity in fish can cause exposed mosquito fish to experience either higher or lower predation depending on the species of predator (Goodyear, 1972; Herting and Witt, 1967). The difference in outcome seems to be due to a difference in the attack behaviour of the predators. This and other possible examples suggest that not only must the category of interactions represented by a test be taxonomically consistent but also the physiological, mechanical, or behavioural mechanisms that control the rate and character of the interaction must be consistent.



The consistency criteria listed above for categories of species interaction tests imply the existence of thousands of categories for which representative predictive tests might be devised. In addition, the importance of a category of interactions must be considered. Importance is defined by the social significance of the organisms involved and the likelihood that they will experience and respond to toxic stress. While an argument can be made for the social significance of any species, there is general recognition of the significance of economic species such as crops, livestock, fisheries, timber, and game species. The likelihood of response is more difficult to define *a priori*. The best evidence that a species interaction is likely to respond to new toxic materials is a frequently observed response to historical ambient pollution. For example, it has been suggested that the fungal or insect attacks of pollution-stressed trees are so common as to be considered a general syndrome (Loucks *et al.*, 1982; Roach, 1979). Less information is available on aquatic systems but the predominance of phytoplankton grazing and predation in aquatic ecosystem energetics suggests that effects on capture efficiency and selectivity could be important.

An additional consideration is the practicality of bringing the species interaction into the laboratory at a reasonable cost. For example, the attack of bark beetles on pollution-stressed conifers may be both important and a consistent category but it cannot be adapted to routine testing because it does not occur in seedling trees. Many other species interactions occur at large spatial or temporal scales or require complex environmental settings.

Currently, multispecies testing can be applied to simple managed systems associated with agriculture, monospecific silviculture, and possibly aquaculture. In such systems, the number of species and the complexity of their interactions are relatively limited. In addition, the economic importance of these systems helps to justify the expense of complex tests. Finally, the species associated with these systems are relatively well understood, available, and easily maintained.

As an example, existing growth tests for crop, timber, or pasture plants could easily incorporate the important symbiotic relationships with root microbes. Growth tests using legumes usually either state that seed should be inoculated or imply inoculation by referring to 'usual cultural practices', but nodulation or other indicators of the success of the association are usually not observed and nitrogen fertilization may be too high for symbiotic nitrogen fixation to affect plant growth. The formation of mycorrhizal associations between plants and fungi is important in plant nutrition and disease resistance. However, mycorrhizal inoculum is not specified in test protocols, and even when plants are grown in field soils the roots are not examined for mycorrhizae formation. Even when effects on the species interaction are most easily detected by monitoring growth of the host plant, as is often the case with the rhizobium-legume symbiosis (Garten, 1985), the presence of the symbiont greatly increases the realism of the test. In addition, even a qualitative evaluation of nodulation and mycorrhizae

formation can increase the interpretive power of a test. Proposed test protocols for the legume–rhizobium symbiosis can be found in Garten (1985) and for both endomycorrhizae and ectomycorrhizae in Suter (1981b).

In addition to generic tests, site-specific tests may be conducted when the toxic material of concern will only be released in one or a few locations or if one of many affected locations supports a particularly valued resource. In such cases, the species interactions that most significantly determine the productivity of socially important species can be identified and tested. For example, the major game fish in a receiving river might be tested for its ability to resist an important parasite or catch local forage fish in the presence of the toxic material.

In summary, it seems likely that some species interaction tests will be useful and even necessary in predictive assessments of environmental toxicology. For the foreseeable future, they are likely to be a rare supplement to assessment strategies based on single species tests and mathematical simulation models. We are only now beginning to identify and quantify the inherent sources of error in such strategies (Suter *et al.*, 1985). Both error analysis and field validation will be necessary to objectively and confidently identify the role of multispecies tests in predictive assessment.

### 3.3 Effluent Monitoring

The third role for environmental effects tests of toxic materials is effluent monitoring. Because the toxicity of a complex effluent often cannot be evaluated by analytical chemistry, particularly when the effluent is diluted in receiving water of variable quality, biological effluent monitoring can be valuable. However, for this use a test should be not only sensitive but also reliable, rapid, inexpensive, and technically undemanding. Single species tests are more likely to display these properties than multispecies tests.

## 4 CONCLUSIONS

Few species interactions are used in routine toxicity testing and the rationale for inclusion of most such tests is weak. The response of interacting species, particularly highly co-evolved species, to toxic materials is highly idiosyncratic so the results of most potential test systems have little predictive generality. The sensitivity to toxic materials displayed by many species interactions in the laboratory is not necessary for screening tests and has generally not been shown to occur in the field. For example, increased fungal and insect attack on trees is observed after pollution is sufficient to cause visible injury to the host tree so that protection of the trees from visible direct pollutant effects would apparently prevent the indirect effects. Finally, a test containing two or a few species will only represent a small fraction of the functional connections in diverse biotic communities. A zooplankton predation test, for example, must be linked to



models or tests for toxic effects on herbivory, algal competition, fish predation, etc., if effects on community dynamics are to be assessed.

The most promising use of species interactions is in higher-level testing for purposes of predicting the type and intensity of toxic effects. However, the problems of predicting effects of toxic materials in multispecies systems are only beginning to be addressed. Models cannot be used to reliably indicate which species interactions should be tested because available ecological models emphasize the processes that appear to be important in the absence of toxicants. Field experience is also a poor guide because few studies have looked at enough species interactions to begin to assess their relative importance. Thus, for complex natural systems, there is a greater immediate need for understanding their responses under toxic stress than for the development of new, more complex tests.

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