Generalized plant defense: effects on multiple species

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Summary. Two species of lepidopteran herbivores, Manduca sexta (Sphingidae) and Trichoplusia ni (Noctuidae), were reared on synthetic diet containing either the alkaloid nicotine or the flavonoid rutin. Survival and pupal weight of the specialist M. sexta did not differ when larvae were reared on diet containing nicotine or rutin. In contrast, the generalist T. ni did not survive on diet containing 0.125% nicotine or greater, whereas larvae survived on all concentrations of rutin. These data demonstrate that the alkaloid nicotine is inhibitory toward generalist, but not specialist herbivores, whereas the flavonoid rutin has no effect on specialist herbivores and limited effects on generalist herbivores. Five species of Pseudomonas bacterial pathogens: P. syringae, P. syringae pv. angulata, P. syringae pv. tabaci, P. fluorescens, and P. solanacearum were grown on nutrient agar containing nicotine or rutin at concentrations ranging from 0.0 to 1.0% wet weight in 0.1% intervals. No species of Pseudomonas grew at concentrations greater than 0.5% nicotine when 10⁶ colony forming units (cfu) were used, but growth occurred at all concentrations of rutin when 10² cfu were used. These data indicate that nicotine was inhibitory to growth of both herbivores and pathogens, suggesting that certain plant secondary chemicals with high toxicity are of a generalized nature and affect multiple species. Differences in the sensitivity of organisms to allelochemicals such as generalist or specialist can make it appear that specific allelochemicals affect specific organisms, when in fact it is the tolerance of the organism to the plant chemical that is responsible. In four separate studies, the growth of M. sexta, T. ni and Helicoverpa zea was significantly lower on plants inoculated with P. solanacearum. Alteration in leaf quality by P. solanacearum was due to either reductions in leaf nutrients or increases in allelochemicals. We speculate that localized or systemic induction by both herbivores and pathogens can cause changes in leaf quality, affecting each other's subsequent colonization. The generalized nature of plant secondary compounds and potential reciprocal effects on induction by both species suggests that herbivores and pathogens may affect plant quality through induction and diffuse interactions of disparate species can alter the community of organisms colonizing a plant.

Key words: Generalized plant defense – Community structure – Pseudomonas sp. – Manduca sexta – Trichoplusia ni

Since Fraenkel's 1959 paper on the purpose of secondary chemicals in plants, a vast literature has accrued which discusses the effects of plant allelochemicals on insects (Rosenthal and Janzen 1979; Denno and McClure 1983). Fraenkel speculated that other organisms such as plant pathogenic bacteria and fungi are affected by secondary plant compounds. The hypothesis that plant pathogens as well as herbivores are selective agents behind the evolution of secondary compounds in plants has been proposed (Whittaker and Feeny 1971; Jermy 1976, 1984; Swain 1974, 1977; Levin 1976; Levinson 1976; McKey 1974, 1979; Rhoades 1979; Zucker 1983). However, very few studies specifically test these speculations that were initially proposed over 25 years ago. Research is needed that evaluates the effects of specific plant allelochemicals on the fitness of both herbivores and pathogens and relates the data to the evolutionary question of whether both constitutive and induced compounds are selected for by herbivores and/or pathogens and whether plant defense is of a general or specific nature (Krischik 1991).

It has been reported that specific plant allelochemicals affect the growth rate of pathogens and the feeding rate and fecundity of herbivores. For instance, the glycoalkaloid tomatine appears to be responsible for the resistance of certain cultivars of tomatoes to Pseudomonas solanacearum (Roddick 1974), which causes Southern bacterial wilt of tomato, potato and other solanaceous plants. Glycoalkaloids in tomato and potato plants are
also implicated as resistance factors to the Colorado potato beetle \textit{Leptinotarsa decemlineata}. The Colorado potato beetle does not grow as well on tomato as on potato (Hare 1983a, b; Hare and Andrædis 1983), and the glycoalkaloid tomatine appears to be responsible for the lower feeding rates of the beetle on tomato (Sinden et al. 1978). Furthermore, the potato glycoalkaloids solanine, chaconine, and solanidine inhibit the radial growth of the pathogen \textit{Alternaria solani} when it is grown on nutrient agar containing these glycoalkaloids (Sinden et al. 1973).

So far we have discussed how herbivore and pathogen fitness may be influenced by the same plant chemicals. In addition, both groups have been shown to alter leaf quality by causing the plant to mobilize chemicals shortly after attack in a process labelled induction. Data demonstrate that induced chemical or phytoalexins can protect plants from both plant pathogens (Afek and Szejteyberg 1988; Caruso and Kuc 1977, 1979; Cruickshank and Mandry 1960; Davis et al. 1986; Guedes et al. 1980; Hardwiger and Webster 1984; Hare 1966, 1983b; Kopp et al. 1989; Kuc 1966, 1972, 1982; Lyon 1984; Sequeira 1983; Stolle et al. 1988) and herbivores (Green and Ryan 1972, 1973; Benz 1977; Baltensweiler et al. 1977; Carroll and Hoffman 1980; Haukojoa and Niemela 1977; Rhoades 1979, 1983a, b; Ryan 1979, 1983; Wallner and Walton 1979; Hart et al. 1983; Schultz and Baldwin 1982; Hare 1983b; Tallow and Krischik 1989). Some authors suggest that a plant’s reaction to damage may not be primarily directed at insects, but plants utilize chemicals with antifungal or anti-bacterial properties (see Hartley and Lawton 1987; Wink 1985). If a plant chemical has a generalized effect on multiple species, then pathogen or herbivore attack may affect the ability of either group to subsequently colonize the plant if induced chemicals act as defenses (for an opposing view on induction, see Fowler and Lawton 1985). Recent research by Karban (1987), Karban and Carey (1984), and Karban et al. (1987) demonstrate reciprocal affects on mites and a \textit{Verticillum} wilt disease caused by induction of resistance in cotton by either the mite or the fungus. Also, work by Kogan and Paxton (1983) shows that the fungus \textit{Phytophthora megasperma} induces allelochemicals in soybean that affect the feeding rates of the Mexican bean beetle. It has been reported that growth of herbivores, bacteria, and fungal pathogens is inhibited by quinolizidine alkaloids present in lupines (Wink 1984). Allelochemical in other plants such as red pepper (\textit{Capsicum frutescens}) and a medicinal herb \textit{Tetradentia riparens} exhibit dual insecticidal and fungicidal properties (Munyemana 1986; Van Puyvelde 1986).

It is clear from the literature that constitutive and induced plant chemicals can reduce the growth rates, feeding rates, and/or survival of specialist and generalist herbivores, plant pathogens, as well as insect pathogens (see Krischik et al. 1988; Krischik 1991). However, the effects of allelochemicals on these groups have seldom been investigated in one system to evaluate the question of whether plant chemicals have a generalized “diffuse” effect on a number of species or affect only certain species. In this paper we study the effects of plant secondary compounds on plant pathogens and herbivores. If the same plant secondary compound affects herbivores as well as pathogens, then we may conclude that plant defense is of a general and not specific nature. Depending on the sensitivity of an organism to a plant chemical, the plant may or may not be colonized. The sensitivity of the species to the plant chemical may give the appearance of a specialized plant compound against a specific organism when in reality only certain plant allelochemicals are involved. We argue that induction of either plant chemicals or alterations in leaf quality by herbivore or pathogen attack can alter the suitability of the resource for subsequent colonization by either group. These diffuse interactions between very different organisms can potentially alter the community structure of insects and pathogens on a plant.

**Materials and methods**

**The organisms**

In order to investigate the specialized or generalized effect of plant secondary compounds, a suite of generalist and specialist herbivores and plant pathogens and their responses to the alkaloid nicotine and the flavonoid rutin were studied. Nicotine is reported in the literature to have toxicity to generalist herbivores while rutin is much less toxic (see Bernays and Chapman 1978; Chapman 1974; Krischik et al. 1988; Krischik 1991).

Tobacco is a host for the tobacco hornworm \textit{Manduca sexta}, a specialist on plants in the family Solanaceae such as tobacco and tomato (Yamamoto and Fraenkkel 1960). The tobacco hornworm is adapted to nicotine and can tolerate high concentrations of the alkaloid (Yang and Guthrie 1969). The cabbage looper, \textit{Trichoplusia ni} and tomato fruitworm, \textit{Helicoverpa ze}, are both generalists and feed on tobacco and tomato, as well as numerous other plants (Metcalf and Flint 1962). These three species are used to determine the effects of constitutive and induced chemicals on generalist and specialist herbivores.

Also, tobacco is a host for both generalist and specialist bacterial leaf pathogens in the genus \textit{Pseudomonas}. \textit{P. solanacearum} causes a disease known as bacterial wilt in species in the family Solanaceae such as tomato, potato, and tobacco as well as other plant families (Kelman 1953). Evidently, \textit{P. solanacearum} growth is not deterred by levels of nicotine that are found in wild tobacco species, since screening studies did not demonstrate many wild species with resistance to this bacterial pathogen (Clayton 1942). However, resistance to \textit{P. solanacearum} is found in \textit{Lycopersicon pinnellifolium}, a species related to tomato, where higher concentrations of the alkaloid tomatine are shown to confer resistance (Rodick 1974). Infections of \textit{P. solanacearum} are systemic and the disease can spread to an entire plant from a single infection site on one leaf. \textit{P. syringae pv. syringae} and \textit{P. syringae pv. angulara} attack numerous crop plants in a number of families and can be considered as generalist pathogens (Kelman 1953, 1954) while strains of \textit{P. syringae pv. tabaci} are more specialized and cause angular and wildfire leaf spot disease of tobacco (Deall and Cole 1986). \textit{P. fluorescens} is a facultative pathogen attacking stored grains and fruits (Kelman 1953). When these \textit{Pseudomonas} pathogens are injected into tobacco leaves, using the method of Klement (1977), distinct lesions develop (see Dowler and Peterson 1980). These bacterial isolates can be used to determine if pathogen infection of a plant affects the growth rates of generalist and specialist herbivores.

Concentrations of nicotine in tobacco foliage range from 0 to 3.6% wet weight in domestic cultivars (Sisson and Saunders 1982, 1983) and to 4.8% wet weight in some wild species (Vanden-