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The Study of Herbivory and Plant Resistance in Natural and Agricultural Ecosystems

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1. Introduction

The successful perpetuation of an arthropod herbivore for part or all of its life cycle on a plant- the use of a plant as a host - is typically the result of a complex and multifaceted process. At each step in the process, the herbivore interacts not only with the potential host plant but also directly or indirectly with other organisms at the same trophic level, such as competing herbivores, and with organisms at different trophic levels, such as predators and parasitoids. A great diversity of plant traits may affect these interactions and, moreover, different plant traits may be relevant at different steps in the process; visual and odor cues emitted by the plant, for example, may be used by herbivores (and natural enemies) for long- or mid-range host location, whereas non-volatile secondary chemicals may be involved in the process only after the herbivore begins to feed on the plant. Any plant trait that varies among individual plants and that affects an aspect of the herbivore's interaction with the plant or with other organisms associated with the plant is potentially a basis for differences among plants in the level of damage caused by the herbivore (i.e., plant resistance). Thus, the study of plant resistance involves the study of a large web of interactions mediated by a potentially large and diverse set of plant traits, and plant resistance can be studied from various perspectives.

Over 25 years ago, Kogan [1] noted the existence of two parallel bodies of research and theory related to the study of plant resistance. The first, which he referred to as the "Insect-Plant Interactions" (IPI) literature, was concerned with describing and explaining the ecological and evolutionary relationships among the two most diverse groups of terrestrial organisms, with a particular emphasis on explaining patterns of variation in the expression of resistance-related traits among plants. The second, which he termed the "Host-Plant Resistance" (HPR) literature, was the province of practically oriented scientists concerned with the development and deployment of crop varieties resistant to herbivores. As these two

bodies of research and theory deal with similar biological phenomena, researchers in the two fields have much to learn from one another. Historically, however, communication between these two groups has been only partial. A great many advances have been made in both HPR and IPI in the years since Kogan's review, but barriers to the exchange of ideas and data among these two groups of scientists still exist, and reconciliation of the two literatures has not yet been completed.

Reconciliation of the HPR and IPI literatures is a matter of considerable practical as well as academic interest. Insect pests significantly reduce the yield and quality of all major plant commodities [2], and the use of insecticides to control insect pests is attended by numerous problems, including high costs associated with both product and product application, elimination of populations of natural enemies, development of insecticide resistance and resurgence by target pests, insecticide-induced emergence of destructive secondary pests, and negative impacts of insecticides on human health and the environment [3]. Increased understanding of the ecology of plant-insect interactions and the proper application of this understanding to crop-pest interactions has led in the past, and will lead in the future, to more effective, less damaging means of managing pests, including the development of resistant crop varieties. The purpose of this chapter is to draw renewed attention to the problematic relationship between the IPI and HPR literatures and to the barriers to the exchange of ideas and data among the two literatures. To that end, I will proceed by first considering the conceptual foundations of IPI and HPR research and then by considering the categorical frameworks under which research in IPI and HPR is conducted. I will conclude with suggestions for applying insights and advances from the IPI literature over the past few decades to HPR research.

2. The conceptual foundations of IPI and HPR research

The seminal work in the establishment of HPR as a distinct discipline was Reginald Painter's *Insect Resistance in Crop Plants*, first published in 1951 [4]. *Insect resistance* is striking for its sophisticated understanding of the complexities of crop plant-pest interactions and for its prescience (with respect to the latter point, the importance to plant resistance of plant phenotypic plasticity and plant tolerance were both points made by Painter but not picked up in the IPI literature until later). Painter's book is also striking because it is bereft of connections to broader ecological or evolutionary theory beyond general applications of the principle of natural selection. Following Painter's lead, most HPR research has retained a heavily empirical and practical orientation, typified by the following statement of Painter's: "The agronomist does not demand a full knowledge of the causes of high yield before breeding for this character in field crops. It is no more necessary to know the exact cause in breeding for insect resistance." [4, pg. 75]

The IPI literature, in contrast, is characterized by a rich tradition of generating and testing hypotheses designed to explain patterns in plant-insect interactions. Although many papers played important roles in establishing the discipline of IPI, two of undoubted importance were those by Fraenkel in 1959 [5] and Ehrlich and Raven in 1964 [6-9]. The paper by

Fraenkel established the focus in the IPI literature on secondary plant metabolites as the primary mediators of plant-insect interactions and also contained inchoate ideas of reciprocal evolutionary relationships among plants and plant-feeding insects [7, 10]. Ehrlich and Raven further developed the concept of plant-insect coevolution in which herbivores and plants were viewed as important drivers of one another's evolution. These authors argued that the fitness-reducing effects of herbivores on plants has selected for the evolution of novel defensive traits in plants, and that the possession of effective defenses by plants has selected for the evolution by insects of adaptations allowing them to overcome these novel plant traits. The evolution of countermeasures to plant defenses by herbivores has acted, in turn, as a selective pressure for the development of further plant defenses, and so on in an escalating reciprocal fashion. According to Ehrlich and Raven, this coevolutionary arms race involving "novel defensive breakthroughs" in plants and "offensive innovations" by herbivores [11] has shaped patterns of variation in plant defense and has served as an important impetus for specialization and diversification in both herbivorous insects and plants.

The ideas of Fraenkel and Ehrlich and Raven have proven to be very fertile and have spawned a number of more specific hypotheses designed to explain patterns of variation in expression of plant defenses at various taxonomic, spatial, and temporal scales [7]. The most influential of these hypotheses have been the optimal defense hypothesis, the growth rate hypothesis, the carbon:nutrient balance hypothesis, and the growth-differentiation balance hypothesis [8, 12]. According to the optimal defense hypothesis, plant defenses at different spatial and taxonomic scales are allocated in a manner that optimizes plant fitness by minimizing the costs and maximizing the benefits of defense expression. The carbon:nutrient balance hypothesis views phenotypic variation in allocation to plant defense as a result of the supply of carbon and nutrients (primarily N) in the environment. The growth rate hypothesis focuses on inherent plant growth rate, itself determined in evolutionary time by resource availability, as the most important determinant of investment in plant defense. Finally, the growth-differentiation balance hypothesis views allocation to plant defense in light of a tradeoff between plant growth and differentiation. Stamp [8] provides a thorough overview of these hypotheses.

Various revisions of these ideas have of course been made in the past five decades. The importance of plant primary metabolites and morphological traits for plant defense has been recognized (10). Also, it has become apparent that the defensive phenotypes of most plants have been shaped by the need to defend against multiple types of attackers simultaneously and thus "diffuse" coevolution is probable more common than the "escape-and-radiate" or "pairwise" coevolution envisioned by Ehrlich and Raven and others [10,11,13]. It has also become apparent that the influence of plant defenses on insect evolution has probably been stronger than the influence of insects on plant evolution [11]. Furthermore, experimental support for all of the specific hypotheses developed to explain patterns of plant defense allocation has been equivocal; although none of these hypotheses has been fully rejected, none of them provides the level of generality desired and enthusiasm for testing these hypotheses has flagged somewhat in recent years [7,8]. These various revisions and

developments notwithstanding, the overall paradigm of a coevolutionary arms race between plants and herbivores mediated largely by plant secondary metabolites remains strongly entrenched as the guiding paradigm for IPI research.

Given the slim conceptual underpinning of HPR research, the real issue in reconciling the conceptual foundations of HPR and IPI research is the extent to which IPI theory is applicable to the study of crop plant-insect pest interactions. Kogan [1] appeared to believe the application of IPI theory to crop plant-pest interactions to be a relatively straightforward matter, and he presents an extended discussion of the application of optimal defense theory to crop-pest interactions. Other reviews, including reviews more recent than Kogan's, often discuss crop-pest interactions in the context of IPI theory [e.g., 14-16], even if they do not attempt detailed applications of plant defense hypotheses to crop-pest interactions.

However, there are at least two major problems with the application of IPI theory to crop plant-pest systems. The first major problem with the application of IPI theory to crop-pest systems arises from the fact that crop plants are often grown in environments very different from those present before or during the process of domestication, when coevolutionary relationships presumably developed. Crop plants are often grown in areas where they are not native, distant from their centers of origin and domestication, and thus are exposed to herbivores and other organisms with which they have no history, or only a relatively short history, of interacting. Crop plants are, in other words, exotic species in most areas where they are cultivated. Furthermore, the conditions that characterize many modern agricultural regions—large monocultures, with abundant water and high levels of fertilizer and other chemical inputs—differ from the conditions present during the process of coevolution of the crop's progenitor with herbivores. Under these circumstances, it is unclear how applicable all but the loosest notions of diffuse coevolution are to crop-pest systems, and how adapted we should expect crop plants and their insect pests to be to one another. A similar point, but applied to biological control, has been made by Hawkins et al. (17). These authors argued that biological control of pests by predators and parasitoids in crops may not reflect predator-prey interactions in natural systems, because food webs present in agricultural systems are often greatly simplified and composed largely or entirely of exotic species, and because the environments in which biological control takes place are greatly simplified in structure and ecological connectedness relative to natural systems.

The second problem with the straightforward application of IPI theory to agricultural systems arises from the fact that crop plants are domesticated, meaning their genotypes and phenotypes have been shaped not only by natural selection but also by human-guided artificial selection. Artificial selection for desired agronomic traits has quite likely altered or disrupted suites of plant resistance-related traits developed over long periods of coevolution with herbivores. This is, of course, obvious in those crop varieties that have been intentionally bred for resistance to herbivores. In these varieties, selection during breeding has resulted in the accentuation of specific resistance-related traits that reduce the impact of herbivory on crop yield, whether or not those traits are fully understood. Importantly, these resistance-related traits may or may not be the same traits favored in the absence of human

action. Prominent examples of intentionally selected resistance include wheat varieties resistant to Hessian fly and maize varieties resistant to various Lepidopteran borers and defoliators; Smith and Clement (16) provide additional examples.

In addition to those cases in which crop plants have been intentionally bred for resistance, there is now ample evidence for collateral effects of selection for desired agronomic traits on crop plant resistance to insects. In some cases, the collateral effects of selection for agronomic traits on plant resistance are easily understood and somewhat predictable because they involve plant traits related to human nutrition or palatability (18). Such appears to be the case in many Solanaceous crops, in which the potential human toxicity of glycoalkaloids has led to the intentional selection of varieties with low levels of these secondary chemicals and reduced levels of resistance to some herbivores and pathogens (19). Similarly, domestication of celery has probably involved selection for reduced levels of furanocoumarins, which can have toxic and irritant effects on humans (20) but which may be involved in the resistance of celery to pests.

Probably more common are those cases in which pleiotropy and epistasis result in unintended collateral effects on plant resistance during breeding (21). Notably, in many crops, selection for increased allocation to agronomic yield and quality appears to have resulted in reduced allocation to defense. There are now a number of studies showing greater susceptibility to pests in domesticated varieties, although the precise phenotypic manifestations of this tradeoff are varied and not as yet predictable. In one of the best-studied examples, a negative relationship was found in maize between degree of domestication and defense against insects; plant growth and yields were highest but resistance to an assemblage of pests lowest in a modern maize cultivar and a land race, whereas growth and yield were lowest but pest resistance highest in annual and perennial wild *Zea* species (18). Resistance to stem borers in wild and perennial relatives of cultivated maize was attributable to greater numbers of tillers in wild varieties, which allowed the plant to compartmentalize injury by borers and thereby minimize yield losses. Wild tomato was more tolerant of defoliation than a domesticated tomato variety, possibly because of higher allocation to leaves and fruits and lower allocation to storage organs in the domesticated tomato (22). In cranberry, resistance to gypsy moth was lower on more derived, higher-yielding varieties than on wild selections (23). The reduced resistance in more derived varieties was correlated to some extent with reduced induction of sesquiterpenes and reduced levels of jasmonic acid. In sunflower, Mayrose et al. (24) found negative correlations between growth under benign environmental conditions and resistance to *Trichoplusia ni* as evidenced by greater preference for high-yielding domesticated sunflowers than for wild sunflowers. Domesticated sunflowers were also more susceptible to fungal infection and drought stress. Also in sunflower, Michaud and Grant (25) found domesticated sunflowers to be more palatable to, and more susceptible to oviposition by, the cerambycid pest *Dectes texanus* than was a wild sunflower. The greater susceptibility of domesticated sunflower to *D. texanus* was partly attributed reduced resin flow in the domesticated variety, a trait that has been selectively diminished during breeding to facilitate harvesting.

The apparent tendency of domestication to negatively impact plant resistance to herbivores has probably been exacerbated by ignorance of mechanisms of resistance and by neglect in monitoring resistance during the breeding of most crops. Rodriguez-Saona et al. (23), for example, have pointed out that the importance of induced plant volatiles in facilitating the action of natural enemies has only recently been discovered, and the plant traits important to this mechanism of plant defense have probably been altered during selection. This idea is supported by the research of Rasmann et al. [26] who showed that the roots of maize lines developed in North America are incapable of emitting caryophellene following rootworm feeding, a lack that compromises the ability of entomopathogenic nematodes from finding and infecting rootworms. More generally, the importance of plant – natural enemy cooperation is only now being recognized, and it is very likely that these cooperative relationships have been disrupted in domesticated varieties [27]. In sunflower, abundance of sunflower moths (*Homoeosoma electellum*) was much higher and parasitism much lower on a domesticated variety than on wild sunflower. The reason for this disruption in parasitism on domesticated sunflower was related to differences in flower morphology and phenology in domesticated and wild sunflower that affected parasitoid searching behavior and access of parasitoids to larvae (28).

Thus, the processes of domestication and plant breeding have sometimes altered crop plant genotypes and phenotypes in ways that compromise or disrupt natural, co-evolved plant defense mechanisms. Moreover, the conditions under which crops are grown may preclude or interfere with natural defense mechanisms, and the status of many crop plants as exotics means interactions between crops and pests are, from an ecological and evolutionary perspective, novel. As a general implication, this brings into question the straightforward application of IPI theory to HPR research; more specific implications are discussed below.

3. Classification schemes for the study of resistance in the IPI and HPR literatures

Because there exists such a variety of ways by which plants may reduce the impacts of herbivory, HPR and IPI researchers have often found it necessary to place resistance types into categories. As might be expected of two disciplines that differ so markedly in their conceptual foundation, the categorical frameworks developed within the HPR and IPI literatures to classify types of resistance differ. Based on observations of resistance in the field, Painter introduced a three-fold scheme for “dividing” the “phenomena of resistance” (4,16). In Painter’s original scheme, the term “antibiosis” was used to describe adverse effects of resistant plants on herbivore physiology and life histories such as reduced growth, survival, and fecundity. The second category, “non-preference”, comprised those plant traits that affect herbivore behavior in ways that reduce the colonization or acceptance of a plant as a host. Finally, tolerance was defined as the ability of a plant to withstand herbivore injury such that agronomic yields or quality are reduced to a lesser extent than in a less tolerant plant subjected to equivalent injury. Since Painter, the use of “mechanism” to describe these terms has largely been abandoned in favor of “modality” or “category”,

probably in response to increased understanding of the plant traits that underlie the actual mechanisms of plant resistance. Also, in 1978, Kogan and Ortman [29] proposed replacing “non-preference” with the term “antixenosis” to emphasize the similitude of this category with the category of antibiosis. Aside from these minor modifications, however, Painter’s trichotomy has been remarkably influential and is still used widely today. For example, fully half of the articles published in the “Plant Resistance” section of the *Journal of Economic Entomology* in 2011 used the terms to describe the lines or varieties under study.

The IPI literature, in contrast, has not seen the establishment of a more-or-less formal categorization scheme comparable to Painter’s trichotomy. However, over the past two decades, in response to advances in the understanding of mechanisms by which plants reduce the impact of herbivores, a bifurcated scheme has emerged (Figure 1). In this scheme, the term “resistance” is used broadly to comprehend those plant traits that reduce the extent of injury done to a plant by an herbivore, where injury is understood as effects on plant physiological processes resulting from the use by an herbivore of a plant as a host (e.g., removal of photosynthate, reduction in nutrient uptake due to root feeding). The term “tolerance” encompasses those plant traits or physiological processes that lessen the amount of damage resulting per unit injury, where “damage” is to be understood primarily in terms of plant fitness. In addition, the resistance category is often further divided into “constitutive” or “inducible” and “direct” or “indirect”. Constitutive plant resistance is resistance that is expressed irrespective of the prior history of the plant, whereas inducible resistance is resistance only expressed, or expressed to a greater extent, after prior injury (i.e., expression of inducible defenses is contingent on prior attack, whereas constitutive defenses are not). Direct plant resistance refers to those plant traits that have direct (unmediated) effects on herbivore behavior or biology. Indirect plant resistance, in contrast, depends for its effect on the actions of natural enemies. The best-studied examples of indirect plant defenses are volatile organic compounds and extrafloral nectaries that facilitate the activities of natural enemies [30].

In considering the relative merits of the IPI and HPR frameworks for classifying resistance, one relevant question is whether Painter’s trichotomy, which has remained virtually unchanged for the past 60 years, is capable of accommodating recent advances in the understanding of the mechanisms of plant defense. Interestingly, in Painter’s original discussion of mechanisms of resistance, he acknowledged the existence of plant traits that did not appear to fit into his trichotomous scheme (4, pgs. 68-70). One such trait discussed by Painter was the long husks of some corn varieties that served as a barrier to the rice weevil; another such trait was thick walls on the pods of some bean varieties that prevented the stylets of plant bugs from reaching the seeds. In the time since Painter, research has served to reinforce the remarkable diversity of plant traits capable of affecting plant-herbivore interactions and therefore capable of serving as bases of plant resistance. Many of these plant traits do not easily fit the definitions of antibiosis, antixenosis, or tolerance set forth by Painter. A few examples will suffice. Indirect plant defenses— plant traits that act by affecting the behavior of the natural enemies of herbivores— provide a set of examples of plant defenses that do not fit easily within Painter’s trichotomy. Two other examples are

provided by Marquis et al. (31), who showed the resistance of white oak to a leafyiting caterpillar to be related to the spatial distribution of leaves in the canopy and the percentage of leaves touching on another, and Chen et al. (32), who showed that resistance of Douglas fir to the western spruce budworm was related to the phenology of bud burst. Although *ad hoc* modifications of Painter’s categories can be made to accommodate these mechanisms of resistance, this cannot be done without contravening the original intent of Painter’s categories.

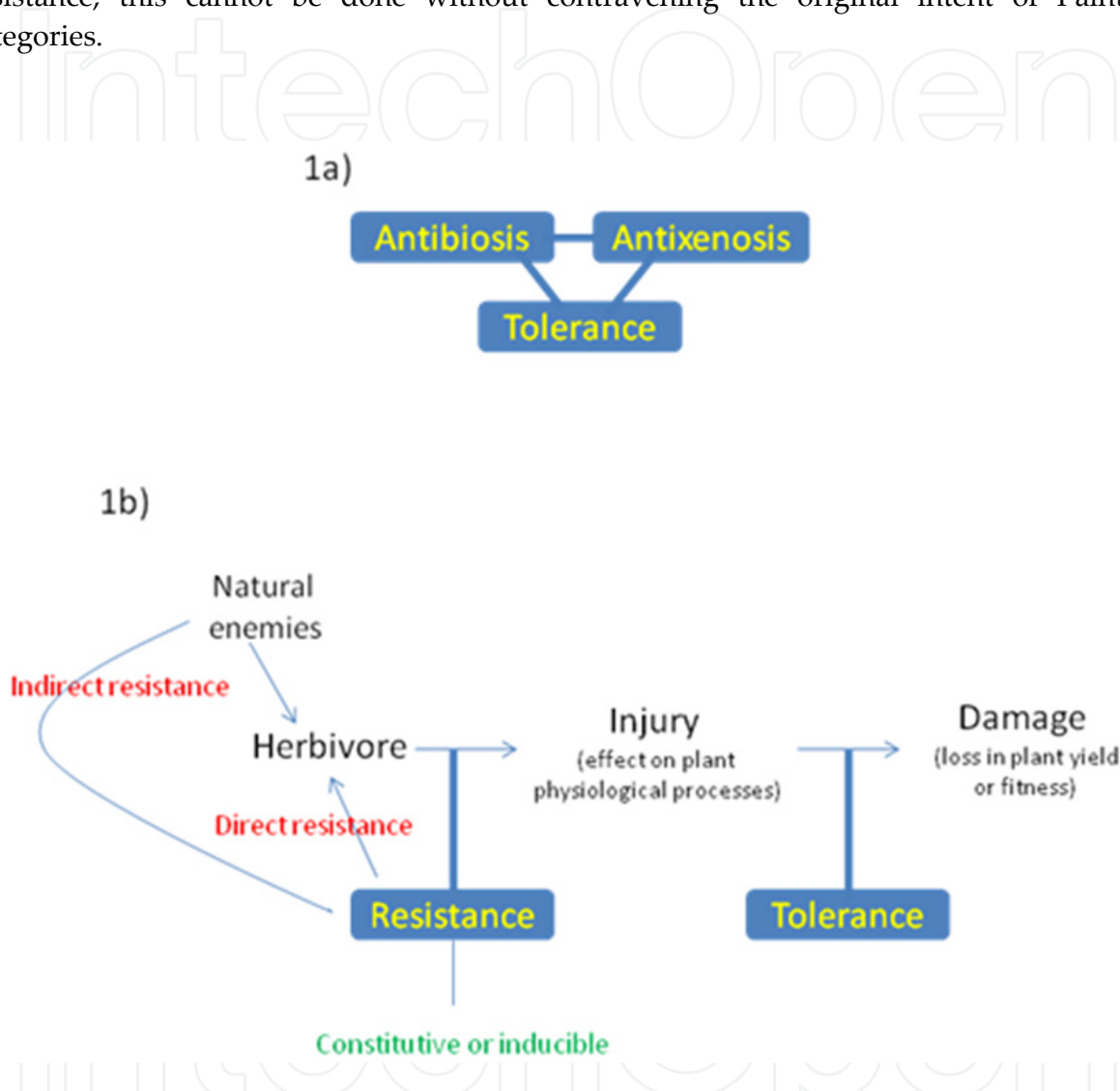


Figure 1. Comparison of the schemes used in the HPR (1a) and IPI (1b) literatures to categorize types of plant resistance to insects.

Another problematic aspect of Painter’s trichotomy involves the antixenosis category and its relationship to antibiosis. In Painter’s original conception, non-preference (antixenosis) was separable from antibiosis, with the two phenomena controlled by different plant genetic factors: The three [categories of resistance] are usually the result of separate genetic factors but are interrelated in their final effects...” [4, pg. 70]. There is, however, some ambiguity in Painter and in the subsequent HPR literature in the use of the terms non-preference and antixenosis. Antixenosis/non-preference has sometimes been used narrowly, to denote

interference with behaviors involved in host location (“pre-alignment” behaviors). At other times, however, the term has been used very broadly to denote effects on behaviors that occur both before a potential host is located and after a potential host is located (“post-alignment” behaviors). When the term is used narrowly, non-antibiotic effects on important pest behaviors involved in the acceptance of host plants for feeding and oviposition are excluded. When the term is used broadly, various difficulties are encountered in separating antixenosis from antibiosis. This is true, for example, when resistance involves a strong element of feeding deterrence; in such cases, antixenosis can be very difficult to distinguish from antibiosis without complicated experimental procedures (33). More generally, research over the 60 years since Painter has shown that the same plant trait often, perhaps even usually, has effects on multiple aspects of a plant-insect interaction, including aspects that might be classified as both antibiotic and antixenotic. As an important example, toxic secondary chemicals are often also deterrent, and vice versa. In fact, a high degree of correspondence between deterrence and toxicity is the expectation of a facile evolutionary analysis, as insects not deterred by a toxic chemical and insects deterred by a non-toxic chemical would seem to be at a selective disadvantage. Experimental tests of this expectation are limited, with some supporting the expectation and other not (34). As another example, the same volatile organic compound emitted by plants after herbivore feeding can attract natural enemies (indirect defense, an antibiosis-like effect), deter oviposition (antixenosis), and perhaps have direct toxic effects on insects (antibiosis) [30,35]. Antibiosis and antixenosis are hence often not separable phenomena but are effects of the same plant traits. In such cases, the results of efforts to categorize resistance often are highly dependent on experimental methods used: choice studies will reveal the resistance as antixenosis, non-choice studies, as antibiosis, even though the same plant trait is responsible for both effects.

Thus, while Painter’s trichotomy has been extremely useful in advancing the science of HPR, it may not satisfactorily accommodate advances in our understanding of the mechanisms of plant resistance. Moreover, Painter’s trichotomy creates a distinction (between antibiosis and antixenosis) that may not be particularly useful, since the two categories involve overlapping plant traits that have the same effect of reducing the amount of injury done by herbivores to crops. The implications of adopting the alternative categorical scheme outlined in Figure 1 are discussed below.

4. Implications

In the above, I have argued first, that the application of IPI theory to HPR may not be a straightforward matter and, second, that the categorical framework historically used by HPR researchers may not accommodate more recent advances in understanding of the mechanistic bases of plant resistance. These are not merely contrarian arguments, but have important implications for the practice of HPR. In what follows, I will seek to point out a few of the implications of these arguments and to suggest areas in need of further research.

4.1. Applying IPI theory to HPR

The issue of the extent to which coevolutionary principles and IPI theory apply to crop-pest interactions deserves more careful consideration. Perhaps the most important questions surrounding this issue relate to the effects of domestication on suites of natural (co-evolved) plant resistance mechanisms. How general is the tradeoff between crop resistance to pests and agronomic yield/quality? Such tradeoffs have now been reported in a number of crop-pest systems, but data are insufficient to conclude that tradeoffs are universal. This is particularly true if negative results (lack of a tradeoff) are less frequently reported in the literature than positive results, which seems likely. Further, when a tradeoff is present, how is the tradeoff manifested? Are certain types of resistance-related traits in plants (e.g., plant traits involved in tolerance, or traits involved in indirect defense) more likely to have been affected by domestication than others? Can patterns in the effects of domestication on resistance be discerned among different types of crops and pests? These and other questions need to be addressed to determine the extent to which domestication has altered natural suites of plant defenses, and to determine whether the effects of breeding are so far-reaching as to preclude the study of crop resistance as a natural phenomenon.

Another important question in the application of IPI theory to HPR is whether the conditions under which crop plants are typically grown make certain natural strategies of defense less effective or unavailable. For example, as Kogan [1] pointed out, the strategy of escaping injury by herbivores by being small or short lived (unapparent) may be integral to the defensive strategies of some plants (including the progenitors of some crop plants) in natural environments, but this is a strategy unavailable to crop plants grown in large monocultures. Similarly, indirect defenses, which are contingent on the activities of natural enemies, may be compromised in the simplified habitats and food webs found in agricultural fields [17].

Finally, what implications are there to the fact that crop plants are subject to attack by pests with which they share only a short history of interacting? One possible implication is that crop-pest interactions may differ qualitatively depending on whether the crop is grown near its center of domestication or elsewhere. In tropical Asia, for example, rice has a long history of domestication, probably long enough for it to co-evolve with its pests and associated organisms, and in these areas populations of many pests on locally adapted varieties are maintained below damaging levels by a combination of top-down and bottom-up factors unless disrupted by early season insecticide use or other high-input practices (36). In contrast, in temperate areas, where rice has been more recently introduced, such natural controls of pest populations appear to be more limited (Stout, personal observations). Another possible implication of the exotic nature of many crop-pest interactions relates to plant defenses triggered by the release of specific elicitors in insect oral secretions (so-called herbivore-associated molecular patterns, or HAMPs). The presence of HAMPs in the oral secretions of insects is viewed as an outcome of the “350 million-year period of coexistence, plants, insects, and other arthropods” (i.e., an outcome of coevolution) [14]. If this is the

case, what level of specificity is to be expected in HAMP-mediated responses of crop plants to pests with which they share no history of coevolution?

4.2. Modifying the categorical framework of HPR research

The categorical framework under which HPR research is conducted needs to be re-examined and perhaps abandoned in favor of a scheme similar to that used in the IPI literature (Figure 1). One effect of adopting the dichotomous scheme used in the IPI literature would be to eliminate the difficulties in separating antibiosis and antixenosis. Another reason is that the “resistance” category in the IPI scheme explicitly incorporates indirect defenses and induced defenses, while Painter’s trichotomy does not. In our current understanding, these are important modes or types of plant defense but are at risk of being ignored in a scheme that does not explicitly recognize them. Inclusion of indirect and induced defenses is important from a practical perspective as well. This is because these types of defenses may require the development of specific phenotyping procedures to monitor for them during the breeding process. Again, such methods are at risk of not being developed until the importance of these types of defenses is recognized.

Adoption of the scheme presented in Figure 1 may also have the salutary effect of focusing more attention on questions of relevance to pest management. As noted above, the plant traits (mechanisms) responsible for antibiosis and antixenosis often overlap, as is the case with secondary plant substances that are both deterrent and toxic. In these cases, efforts to categorize resistance as antibiosis or antixenosis may be counterproductive because they divert attention and resources from the critical question of how a particular plant trait effects a “reduction in the over-all population of the insect resisted” [4, pg. 49] by altering the biology or behavior of the pest or of other organisms associated with the plant-pest interaction. An antibiotic trait that slows the growth and development of a Lepidopteran pest may reduce pest populations to a much lesser degree than antibiotic trait that kills a large portion of early instars. Alternatively, the two antibiotic traits might bring about similar population reductions by very different mechanisms—the former trait, by direct effects on the pest; the latter trait, by synergizing the effects of natural enemies. Or, an antixenotic trait that strongly deters insect feeding, resulting in pest starvation, and an antibiotic trait that poisons a pest may reduce pest populations to similar degrees. In all these cases, the status of a trait as “antibiotic” or “antixenotic” is far less important than the mechanism by which the traits bring about reductions in pest populations the reduce injury to the crop. Recent advances in genetic manipulative techniques have made it feasible to alter plant traits with precision and to monitor the effects of such alterations on pest populations, making categorization of resistance types less important.

5. Conclusions

The promise of increasing crop plant yields and food production by developing and deploying insect-resistant crops remains partly if not largely unfulfilled [16,33]. Great technical strides have been made over the past few decades in the ability to identify and

quantify secondary chemicals and other plant traits associated with plant resistance. Likewise, great strides have been made in the ability to alter expression of specific plant traits through manipulative genetic methods. These advances enable us to investigate how the presence of specific plant traits change the interactions of pests with crop plants and with associated organisms and how these changes result in reduced crop injury and damage. What is particularly needed now is an understanding of the full array of strategies by which plants lessen the impact of herbivory in natural habitats, and an understanding of how domestication and modern agronomic practices have affected this array. This task will be facilitated by the use of terminology and categories that encompass the range of strategies used by plants. Ultimately, this undertaking may allow reversal of the effects of domestication and modern cultivation practices by target breeding, genetic engineering, alteration of crop environments, and other tactics.

Author details

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