

Variable Host Resistance to Moderate and Catastrophic Damage Causing Insects and Diseases

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Trees have been at a proverbial war with fungi and insects just about since their inception. Each combatant brings a different set of tactics to the table in an effort to overcome its adversaries. It might even be convenient to refer to this arrangement as a predator-prey situation, in which trees are vulnerable stationary prey and insects and fungi are opportunistic predators just looking for the resources they need to survive. Do trees need to live in the absence of attack to survive and thrive, or is it enough to just tolerate the damage just to get by, a sort of 'win-win' for all parties involved because the tree remains alive and the insects and fungi get the nourishment they require. Variable host resistance in trees is a complicated issue littered with pitfalls of exceptions and areas void of understanding. Perhaps through careful presentation of the basics of host resistance and the use of examples for moderate and catastrophic damage causing insects and diseases we can pull apart some of the mechanisms behind variable resistance or at the very least start to notice some patterns even if we cannot fully explain why.

INTRODCUTION

Defining the Basics

Resistance, tolerance, and immunity are all terms used in the literature to describe varying aspects of plant defense, but since the definitions can vary from text to text it is necessary that I define these as well as a few other concepts. Immunity, or absolute resistance, is a rare and precious quality that should be used and deployed with care and caution. Immunity is often brought up in discussions of breeding programs, but it is often not the goal like many think (Zobel 1982). Similar to immunity, resistance has its roots in breeding research. Resistance, simply put, is any characteristic that will minimize damage, be it toxins, deterrents, or compensatory processes (Larsson 2002). Less studied is the role of tolerance, although research in the last decade has emphasized its importance. Tolerance has

a close relationship with resistance in that compensatory processes which I previously classified as resistant traits are in fact tolerant traits. I will often refer to tolerance as separate from resistance, but ultimately tolerance is a form of resistance. A good way to conceptualize this would be that tolerance is a form of resistance, but not vis versa. Similar to how a thumb is a finger, but a finger is not a thumb. A good reason to keep them separate would be that resistance and tolerance seem to be alternatives. They both carry costs and are not able to be maximized both at the same time within an individual, or often within a single genotype. Still our understanding of tolerance lags behind that of resistance, despite the possibility that tolerance may be much more important than generally acknowledged.

Resistance

Perhaps the broadest definition of resistance is “the ability of an organism to withstand or oppose the operations of or to lessen or overcome the effects of an injurious or pathogen factor” (Committee on Technical Words 1940). Such a definition includes both the effect of the plant on retarding pathogen growth (resistance) and the ability of the plant to either avoid disease or to function despite high disease levels (tolerance). Resistance often focuses on the negative effect a resistant plant's trait has on the target herbivorous insect or disease; but it is important to separate the concept of resistance into two parts: the plant trait and the target insect or disease. Resistance is a culmination of the plant component, the resistant trait, and the insect or disease's response to this trait. Diseases will generally only have physiological responses whereas in the case of insects, due to complex behaviors, the response can be behavioral in addition to physiological.

A resistant trait such as a toxic chemical, trichomes, or thick bark could have evolved in response to a myriad of selection pressures, such as UV-radiation, frost, drought, microorganisms, mammals, plant competition, as well as insects and diseases. For insects, the negative effect on the attacking individual can be two kinds. It can either (*i*) result in an avoidance behavior, oviposition, or feeding,

whereby the insect is deterred by the plant trait (antienosis); or alternatively (ii) the resistance trait can interfere with the physiology of the insect, once it has committed to feeding on the plant, leading to reduced growth, fecundity, or survival (Larsson 2002).

Caveats

Not every plant escapes insect herbivory or infection by disease due to its defenses or ability to tolerate antagonism. In plant pathology, “non-host resistance” is a term used to describe the inability of a pathogen to infect a plant due to a lack of something in the plant that the pathogen needs or the presence of substrates incompatible with the pathogen. The term non-host resistance is seldom used in insect literature, although the avoidance behavior shown by an insect to a plant that is not part of its host range is highly analogous to non-host resistance against microorganisms (Larsson 2002).

It is important to remember that a plant being resistant does not necessarily mean it will be damaged any less than a more susceptible plant, though this is often the case. This is not always immediately intuitive, but for example if a particular resistance trait has sub-lethal effects on an insect's growth, the subsequent effect may be compensatory feeding by the insect whereby more plant tissue is consumed on a resistant plant than a less resistant one.

Inheritance of Resistance

Resistance has long been considered to be genetically controlled, most likely due to the strong influence from agricultural plant breeders early on. More recently, ecologists have used resistance more broadly. It is frequently referred to as a phenotypic feature possibly shaped by biotic as well as abiotic factors, similar to the nature versus nurture axiom. Inheritance of resistance in plants to particular pathogens is often race-specific, meaning inoculation of plants with some isolates produce resistant reactions while inoculation of others results in susceptible reactions (Alexander 1992). It is generally accepted that resistance traits seem to be at least in part genetically controlled, but whether these traits

are controlled by a single gene or multiple genes is still debated on a per host-antagonist interaction basis.

Effects of Disease on Plant Fitness

As discussed earlier, a resistant plant is not necessarily less likely to be attacked, which is not very intuitive. Similarly, just because a plant is attacked, it does not mean that the disease or insect will reduce the plant's fitness. Unfortunately due to the widespread belief that attacks on a plant will certainly result in reduced its fitness, there is very limited data on the effects of disease and insect herbivory on plant fitness in natural populations. Fitness being defined here as the expected contribution of a phenotype compared to contributions of other phenotypes. The importance of insects and pathogens may vary at different stages of the life cycle of plants, with differing effects on fitness. Though the effects of disease may not be immediately evident. For instance, in the case of annuals where fitness is often measured by the number of seeds produced in a single generation, disease effects may be underestimated if seeds from diseased plants are reduced in size, affecting the success subsequent generations while not effecting the number of seeds counted (Alexander 1992).

RESISTANCE TRAITS

Primary Metabolites

Nitrogen is by far the most important nutrient for insect growth and development and ultimately survival. Many insects have evolved life histories that maximize nitrogen uptake from plant tissues low in nitrogen in comparison to their needs (Larsson 2002). This is particularly important in the case of beech bark disease (*Cryptococcus fagisuga* + *Nectria spp.*) where bark of resistant American beeches has significantly lower concentrations of some amino acids and total amino nitrogen than does the bark of uninfested bark of susceptible trees (Houston 1994). Since amino nitrogen is such a major limiting

nutrient in the nutrition of sucking insects, including the beech scale involved in this disease complex, the likelihood of attack is reduced due to insufficient resources (non-host resistance). Perhaps the catastrophic nature of this disease complex is due in part to the fact that this type of resistance is constitutive in nature and cannot be induced in the single lifetime of a tree but rather is brought about through an evolutionary timescale. But it is worth noting that plant-feeding insects are likely sensitive to the composition of nitrogenous compounds, therefore total nitrogen can be misleading when determining the suitability of a particular plant for insect feeding (Larsson 2002).

Carbohydrates have been relatively overlooked in plant/insect studies, most likely due to the assumption that energy does not limit growth for herbivorous insects, though there is evidence to the contrary. For example, studies have shown that single carbohydrate compounds are essential ingredients in the food of arboreal caterpillars. Heterogeneity of habitats, differences in age within a species, as well as differences among tissue types within plant individuals all contribute to variation seen in concentrations of primary metabolites in plant species (Larsson 2002). Because so much variation seems to be of ontogenetic and physiological origin, primary metabolites are rarely considered part of plant resistance, although this may be erroneous.

Secondary Metabolites

Genetic variation in secondary metabolites such as terpenoids, phenolics, and alkaloids and the negative effects that these compounds have on insect performance has been well documented (Larsson 2002). In comparison to primary metabolites, there is tremendous interspecific variation in the composition and concentration of secondary metabolites. In addition to the interspecific variation, there is also considerable variation among plant individuals of different age, among branches within the canopy, and among leaf ages within individual branches.

Unlike primary metabolites, secondary metabolites are not essential for insect growth and

development. In fact they are highly toxic to insects. To combat this, insects have evolved behavioral adaptations to avoid the toxic chemicals, or in some cases, efficient detoxification systems. Presumably, biochemical adaptations, such as a detoxification systems, are extremely costly for the insect and are considered to be the prime reason for the widespread specificity in plant use among herbivorous insects (Larsson 2002). However, other phenomena, such as escape from natural enemies, are also likely to contribute greatly to the high degree of host specialization among herbivorous insects.

Secondary metabolites may be constitutive, meaning there are always present in the plant, or occasionally induced by insect feeding. For example, species resistant to attack by emerald ash borer (*Argilus planipennis*) have developed, through co-evolution, qualitative and quantitative variation in their constitutive secondary chemistry of their phloem relative to that of the susceptible native U.S. species which may contribute to their resistance (Rebeck et al. 2008). This may point to why the emerald ash borer is such a catastrophic species. Without the opportunity to co-evolve with the insect, native U.S. species are behind in an evolutionary sense are completely unable to catch up or defend themselves in other ways.

Constitutive compounds are often used as cues by insects and dictate whether or not plants will be selected for feeding or oviposition. Thus for adapted insects, meaning those who have evolved the biochemical machinery to handle feeding on these otherwise toxic plants, secondary metabolites generally do not function as resistance traits, but rather as a guide for the insect to the right plant (Larsson 2002). Yet again this is less than intuitive, because what started as a deterrent became an attractant. But this is not a failure of the plant, but rather a evolutionary success of the insect. Remember though, despite these isolated cases of increased susceptibility, constitutive secondary metabolites otherwise protect the plant from the majority of non-adapted insects as intended. Also worth noting is that even specialist insects can be influenced negatively by high concentrations of secondary compounds in their natural food plant.

The distribution of secondary metabolites among plant species can be explained through two perspectives: evolutionary and ecological. The evolutionary perspective aims to understand patterns of secondary metabolites among plant species with different life histories and varying habitats, emphasizing aspects such as optimality, plant apparency, and resource availability (Larsson 2002). The ecological perspective is predominated by ecophysical explanations, such as hierarchies in allocation of resources, the balance between carbon and nutrient availability, balance between growth and differentiation, and sink/source regulation.

Physical Factors

Insects not only struggle to overcome chemical barriers but physical as well. Toughness of leaves is a serious hurdle for many herbivorous insects, possibly hindering non-adapted insects from investigative feeding, although this source of resistance is often difficult to separate from chemical traits (Larsson 2002). The toughness of leaves on woody plants varies among trees, within taxa among habitats, and among age classes within a species. As with many other topics discussed here, there are some non-intuitive caveats; namely that even an adapted insect may find it difficult to feed on the tough leaves of certain plants.

In addition to leaf toughness, leaves, buds, and young shoots may be covered by small hairs that can be morphologically and functionally very diverse (Larsson 2002). In the case of insects, it is generally assumed that these hairs can act as a resistant trait. Some researchers have even gone as far as to remove all the hairs from young leaves to observe the effect, the result of which was increased accessibility for insect larvae.

Some plants employ a combination of physical and chemical traits through use of trichomes with glands containing secondary metabolites. These glandular trichomes release an exudate that affect insect feeding and movement by the action of trapping or deterring the insect. Many examples of plants using

glandular trichomes to provide resistance against insects exist in agricultural literature (Larsson 2002). These hairs are present on many woody plants, especially in young tissue, though their ecological importance has not been extensively investigated.

Phenology

Many insects are not only specialized on a specific plant toxin but also on a specific plant tissue. This could present a considerable risk to an insect considering that some plant tissues are only available for a short period of time each year, which is the case, for example, with the bud break of perennial plants in temperate regions (Larsson 2002). Much like other resistant traits, there is a considerable amount of variation in the timing of bud break at several spatial levels, i.e., among plant populations, among individuals within a population, among branches within plant individuals, and among buds on a branch. Such variation may have consequences for the growth and survival of associated insects, the strength of such an effect depends greatly on the insect's life history traits, for example degree of tissue specialization, dispersal capacity, and lifespan. In the case of insects with short life spans and an extreme dependence on a specific growth phase, timing is especially important and any variation may prove detrimental to the insects development and ultimately its survival.

In natural systems, insects have evolved life histories that are synchronous with the seasonal development of preferred plant tissue. This means that in most years, most insect individuals will successfully exploit their food sources with only a marginal few being asynchronous. The food sources, i.e. plant individuals, branches, and buds, may also be asynchronous with the majority of the resource population yielding them resistance due to lack of substantial attacks by feeding insects whose timing would normally coincide with their development. This can be seen in the example of basswood thrips (*Trips calcaratus*) where the severity of attack by basswood thrips seems to depend on the synchrony between the thrip's emergence from overwintering sites and bud swelling and opening (Raffa et al.

1992). Perhaps the reason why basswood thrips are only a moderate pest is because seasonal development can be so variable causing an almost constant asynchrony. Exploiting this asynchrony for use in pest management may prove useful, but more research on the subject is still needed.

Seasonal development of shoot length or leaf morphology are often accompanied by changes in chemistry. This is exemplified by the chemistry and development of growing oak leaves where as the leaves mature, protein concentrations decrease and tannin concentrations increase (Larsson 2002). In cases where chemistry has been fully and thoroughly investigated, great changes in concentrations with the aging of plant tissues has always been detected. That is why traits that would normally be labeled “phenological” may actually be chemical or physical in nature.

ACTIVE VERSUS PASSIVE RESISTANCE

Active and passive resistance describe two different strategies by host species for defending against insects and diseases, each with its own unique advantages and disadvantages. Active and passive are also referred to as induced and constitutive respectively in insect and disease literature and the hypothetical relationship between the two and the probability of attack can be seen to the right (Figure 1).

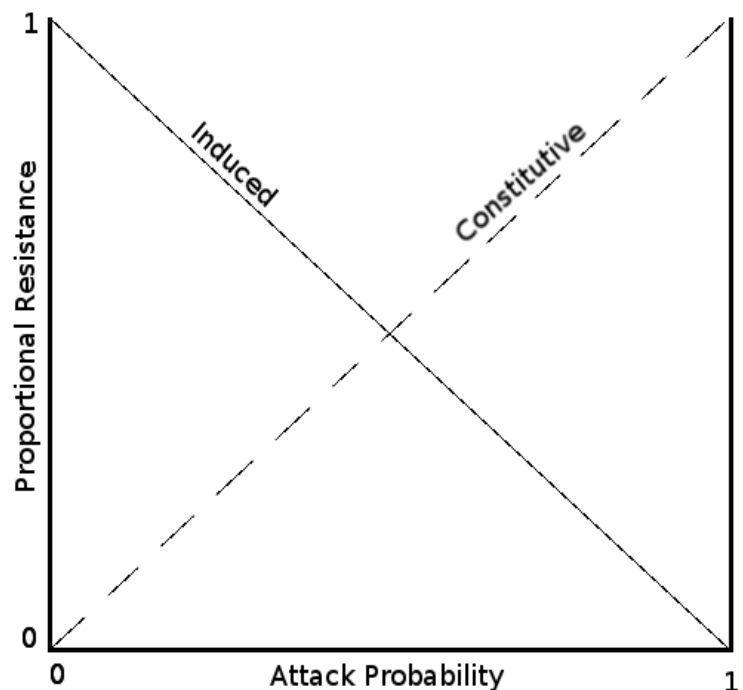


Figure 1. Hypothetical relationship between type of defense and probability of attack.

Active mechanisms of resistance involve a direct physiological or biochemical interaction between plant and insect or pathogen (Alexander 1992). Whereas Passive resistance results when the insect or disease has little effect on the plant because of plant traits that are for the most part independent of the presence of the antagonist. Constitutive traits may, however, be active in an evolutionary sense if they resulted from past selection imposed by insects or pathogens. In the passive mechanism of disease avoidance, genetically controlled plant traits reduce the probability of an encounter between plant and pathogen (Alexander 1992).

There are many examples of active resistance in insect literature. For example, with hemlock woolly adelgid (*Adelges tsugae*), a catastrophic event causing insect, where the insect induces a hypersensitive response which may be a result of where and how it feeds on the plant. Normally hemlocks mounting a successful systemic response could provide new growth needles with more protection from sessile herbivores, but since high hemlock woolly adelgid population densities induce magnified hypersensitive responses in infested tissues, this defensive response that would otherwise be beneficial could become costly and even lethal to the host plant (Radville et al. 2011). In the case of the moderate disease event, white pine blister rust (*Cronartium ribicola*), white pine's resistance to this disease is also a hypersensitive response, but this most likely developed as resistance to endemic pathogens before white pine blister rust was introduced (Kinloch 1991). Perhaps the difference in severity of the two attacks could be due to whether or not the hypersensitive response was developed long before the attack though an evolutionary response to endemic pathogens or if the response was only recently induced by a relatively new insect or disease.

A good example of passive resistance is that to Dutch elm disease (*Ophiostoma ulmi*) where resistant trees naturally defend themselves against the invasion of the Dutch elm disease pathogen by restricting the spread of the fungus in their vessels. Studies have shown that non-adapted trees may also exhibit resistance if first inoculated with a non-aggressive strain of the disease which will induce

resistance to not only the non-aggressive strain but also aggressive strains, thereby protecting it from future attack by aggressive strains that would have otherwise resulted in reduced growth or survival (Hubbes 1999).

DEFENSE THEORIES

Importance of Trade-Offs in Determining Level of Resistance

Central to all defense theories about plant resistance is that there is a cost associated with the production and maintenance of traits associated with resistance. If there is a cost, then there is the potential for trade-offs, often seen as a negative association between two traits in a phenotypic expression. One trade-off that is often brought up is the one between growth and defense. But despite its popularity, the expected negative relationships between these two functions have proven difficult to document (Larsson 2002).

The allocation costs of growth and defense, i.e., costs of production, transport, storage, and maintenance, are brought up most often, but it is important to remember that there are other kinds of costs. For example, opportunity costs occur when a plant cannot successfully compete with rival plants because it has invested in resistant traits too early in its development when there was nothing to defend against. There are also ecological costs that can come about if a trait provides resistance to one disease or insect, but results in increased susceptibility to another, or negatively influences natural enemies or pollinators (Larsson 2002). A much less studied but potentially important trade-off is the one between different kinds of resistance traits. For example, leaf toughness in some plants is negatively correlated with trichome density. The fact that different resistance traits respond differently to environmental factors could also be the result of trade-offs and competition for shared resources. There is much left to be discovered about the trade-offs between growth and resistance and among different resistance traits,

but the more we learn about these relationships, the closer we become to understanding the evolution of resistance.

Optimal Defense Theory

The optimal defense theory assumes that defense will always have a cost. That cost is the fitness impact associated with the loss of a given quantity of tissue and depends on the characteristics of the tissue (Zangerl and Bazzaz 1992), i.e., how expensive the tissue is to the plant. Due to high variation in the severity of attack between specific plant individuals within a population, branches within a canopy, or even between leaves and buds on a branch, it does not make sense for all individuals to always protect themselves because of trade-offs such as opportunity cost. But some plant parts are more likely to be attacked than others so this theory suggests that those with a higher probability of attack are more likely to be protected by the plant.

Resource Availability/Defense Hypothesis

The resource availability/defense hypothesis focuses on the habitat in which a plant grows. In resource-rich habitats, plants with high growth rates are favored. These high growth rates are achieved through the production of nutrient inexpensive leaves that can be quickly and economically replaced as the tree competes in the canopy. Because selection of plants with high growth rates is favored in resource-rich habitats, the indirect costs of defenses for defended plants would place them at a competitive disadvantage compared to undefended plants (Zangerl and Bazzaz 1992). Conversely in resource-poor habitats, plants are characterized by slow growth and long-lived leaves. In this environment, it is much more costly to replace leaves therefore much more energy is invested into defense to avoid leaf loss.

COMPLEX INTERACTIONS

I defined resistance earlier as being composed of two components: the plant trait and the target insect or disease. Although this is true in most cases there are exceptions to this definition. A good example of this is chestnut blight (*Endothia parasitica*) where it is not a host/pathogen interaction that confers resistance but rather the pathogen's interaction with hypovirulent pathogen. In the U.S., chestnut blight is a severe problem, but in Europe the disease may cause a decline in the quality of timber but is not considered much of a problem. This is because Europe has widespread hypovirulence. So in the U.S., attack by chestnut blight is thought to be catastrophic because of a lack of biocontrol rather than a lack of tree resistance. Unfortunately in order to successfully implement this biological control in the U.S., we must first find or produce stable hypovirulent strains of *H. parasitica* (i) that can survive in nature with killing native chestnut trees, (ii) are present in broad ranges of vegetative compatibility, and (iii) are conducive to natural spread (Anagnostakis 1982).

CONCLUSION

Plants defend themselves in many ways, whether it be by means of resistance, tolerance, or immunity. Each strategy comes with its own costs and trade-offs which have been carefully considered by plants through evolutionary history. Resistant traits such as toxic chemicals, trichomes, or thick bark have evolved in response to a myriad of selection pressures, such as UV-radiation, frost, drought, microorganisms, mammals, plant competition, as well as insects and diseases. A plant may even alter its phenology in order to escape attack in a temporal dimension rather than a spatial one adding to the complexity of the interactions between plants and their aggressors. There have been numerous theories proposed to describe and predict resistance but more research needs to be conducted before we fully

understand the evolution of resistance. It is my hope that the information summarized here may serve as a useful guide to others on the basics of variable host resistance, and the contrast of moderate and catastrophic damage causing insects and diseases has provided enough context for these concepts to become more understandable.

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APPENDIX

I completed my internship between two closely related settings in Umeå, Sweden. The first is called the Umeå Plant Science Centre (UPSC), which is a partnership between the Department of Plant Physiology at Umeå University and the Department of Forest Genetics, and Plant Physiology at the Swedish University of Agricultural Sciences (SLU). One of my advisors, and main contact for the internship, Benedicte Albrechtsen works at UPSC. The second lab I work with is at SLU working with my second advisor Michael Gundale under the Department of Forest Ecology and Management. Both of these universities are located in Umeå, Sweden and have a close relationship with each other, sometimes having researches funded by one university, but having their office in the other university. This unique situation proved beneficial for me as the internship was very flexible to my needs and desires.

My learning objectives for my internship were as follows: how to perform statistical analysis of collected data, learn more about nutrient and carbon cycling and budgeting, and what factors influence forest productivity and in what ways. Through my experience in Sweden I completed all of these objectives and while learning much more than I had originally bargained for. By speaking with my advisor I was able to express my interest in GIS and remote sensing and she was able to connect with several different people using GIS in their research, as well as some other researchers who are on the cutting edge of the research in remote sensing. I was also connected with a group researching methods by which to predict the location of red listed species through means of analysis of satellite images and other remote sensing tools. They were training technicians in the field to identify the red listed species so that they could go out on their own and identify them independently. We spent three days near Hemavan, Sweden searching for red listed species. Through that experience I started to notice the complex relationship between topology, climate, and vegetation. There area is rather unique and as a

result contains several endemic species of plants. I included a picture below in an effort to capture the essence of the area.



During my internship I also completed a project assessing the specific the specific leaf area for ten aspen genotypes from the Swedish Aspen (SwAsp) collection. The primary questions answered though the completion of this project were: does genetic variability have any effect on specific leaf area (SLA), in what ways does a gradient of nitrogen conditions affect SLA, and what is the combined effect of the interaction between the genotype and the environment (fertilization level) on SLA? The results were presented in the form a small report including an introduction, methods, results, and discussion section. I also gave a short oral presentation of my work during one of the lab meetings.

In the end I came away from this internship thinking I had one of the best summers of my life. Not only was I able to progress myself academically, but I feel that I grew as a person as well. Having internships as a requirement forced me to step out of my comfort zone and created experiences that will last me a lifetime. I stepped away from this internship knowing more about myself and what career path may look like, which in the end is all the more I could ask for.