

Direct and ecological costs of resistance to herbivory

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Herbivores can consume significant amounts of plant biomass in many environments. Yet plants are not defenseless against such attack. Although defenses might benefit plants in the presence of herbivores, herbivore attack varies both spatially and temporally, and the expression of plant resistance to herbivores can be costly in the absence of plant enemies. Costs can be described as allocation costs, resource-based tradeoffs between resistance and fitness, or as ecological costs, decreases in fitness resulting from interactions with other species. Here, we update the seminal 1996 Bergelson and Purrington review of resistance costs and find that many more studies have documented costs of resistance (*sensu lato*) than found during the 1996 survey. Eighty-two percent of studies in which genetic background is controlled, demonstrate significant fitness reductions associated with herbivore resistance. We categorize studies by type of resistance, induced or constitutive, by type of cost, and also by the degree to which investigators controlled for genetic background. Recent work has commonly detected both direct resistance costs, such as resource-based tradeoffs, and ecological costs, which depend on interactions with other species.

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The principle of allocation, that organisms must partition limited resources among the processes of growth, reproduction and defense, has motivated most of the theory about the evolution of plant defenses against herbivores [1–4]. These theories hinge on the presence of COSTS OF RESISTANCE (see Glossary), because, in the absence of costs, one expects selection to favor the most defended genotypes. Whether costs are expressed can depend on the environment in which the comparisons between resistant and susceptible plants are made, the genetic background in which RESISTANCE traits occur, and on the ecological context in which costs are measured [5]. Costs can arise directly from the resistance trait itself, or indirectly via interactions with other species. DIRECT RESISTANCE COSTS include ALLOCATION (or resource-based) COSTS, auto-toxicity (when resistance traits, such as secondary chemicals, are toxic not only to herbivores, but also to plants), and opportunity costs, which occur when small costs early in plant life history are compounded as plants age [6]. INDIRECT, OR ECOLOGICAL COSTS of resistance require ecological interactions with another species to be expressed (Box 1).

In spite of the importance of costs to plant defense theory, they have been difficult to detect, and some researchers have doubted that they exist [3]. In 1996, Bergelson and Purrington conducted a survey of studies to determine the prevalence of costs of plant resistance [5]. Their study aimed to understand how

test environment and methodologies affected whether costs were detected. Their paper was seminal because it carefully reviewed a large literature and thoroughly discussed the advantages of different methodological approaches to the detection of costs. Bergelson and Purrington [5] considered plant resistance to herbivores, pathogens and herbicides in 58 studies, including 88 comparisons, and found that costs were evident in only 33% of the studies examining plant resistance to herbivores ($n=17$). The lack of resounding evidence for costs was surprising, given that many studies have shown that most plant populations are variable for resistance to herbivory, and that this variation is heritable and thus might respond to selection [7].

Here, we update the Bergelson and Purrington [5] 1996 survey with results from 33 studies from the past six years, and consider costs related to resistance to herbivores only. We show how recent work provides strong evidence for costs, and discuss ecological costs and INDUCED RESISTANCE costs, which have recently received more attention. Finally, we include results from studies that did not control for genetic background previously purposefully omitted by Bergelson and Purrington [5]. We discuss how one might incorporate studies of natural populations into the study of costs and discuss methodological issues related to control of genetic background and the measurement of resistance costs. We present the results in Table 1, which includes all studies addressing CONSTITUTIVE RESISTANCE, and in Table 2, which includes induced resistance studies. Table 3 summarizes the individual explorations within studies by categories of the type of cost (direct, indirect), genetic background (controlled, or not) and the type of resistance (constitutive, induced). Although we focus on plant–herbivore interactions,

Box 1. Types of ecological cost of resistance

- Deterrence of mutualists (pollinators, seed dispersers, predators and parasitoids of herbivores, mycorrhizal fungi, fungal endophytes, root-nodule bacteria, etc.)
- Increased parasite load or impact of enemies (other herbivores, seed predators, nectar robbers, pathogens, etc.)
- Reduced tolerance to enemies (herbivores, seed predators, nectar robbers, pathogens, etc.)
- Reduced intra- or interspecific competitive ability

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Table 1. Studies of costs of constitutive resistance^{a,b}

Plant species	Herbivore species	Reason for cost	Cost type	Magnitude of cost ^c	Fitness measure	Genetic background ^c	P/G ^d	Multiple Refs popul.	
Studies controlling for genetic background									
<i>Brassica rapa</i> (Brassicaceae)	Natural herbivore community	Trichomes	D	$\beta = -0.13$	Flower	S	G	N	[34]
	<i>Phyllotreta cruciferae</i> , <i>P. cruciferae</i> , <i>Leptosphaeria maculans</i>	Myrosinase activity	D	15%	Seed	S	G	N	[35]
		Myrosinase	D	15.5%	Seed	S	G	N	[36]
		Glucosinolates	D	0%	Seed				
	<i>P. cruciferae</i>	Resistance to	D	0%	Seed	R	G	N	[37]
	<i>Ceutorhynchus assimilis</i>	Resistance to <i>C. assimilis</i>	D	0%	Seed				
	<i>Plutella xylostella</i>	Myrosinase	E	40% less time	Pollinator foraging time	S	G	N	[38]
	Simulated herbivory	Glucosinolates	D	32%	Seed	S	G	N	[39]
		Tolerance/resistance tradeoff	E	42–58%	Seed (60% herbivory)				
<i>Ipomoea purpurea</i> (Convolvulaceae)	Natural herbivore community	Tolerance/resistance tradeoff	E	0%	Tolerance	R	G	N	[40]
<i>Cucumis sativus</i> (Cucurbitaceae)	<i>Tetranychus urticae</i> , <i>Diabrotica undecimpunctata</i>	Cucurbitacins	D	0%	Biomass	I	G	N	[30]
		Resistance to <i>Sphenarium purpurascens</i>	D	Quadratic relationship of fitness with resistance	Fruit	R	P	N	[41]
<i>Datura stramonium</i> (Solanaceae)	<i>Epitrix parvula</i>	Resistance to <i>E. parvula</i>	D	0%	Fruit				
		Glandular trichomes	D	45%	Seed	R	P	Y	[24]
Studies not controlling for genetic background									
<i>Pastinaca sativa</i> (Apiaceae)	<i>Depressaria pastinacella</i>	Furanocoumarins	D	$\beta = -0.32$	Seed	N	P	N	[42]
<i>Centaurea solstitialis</i> (Asteraceae)	Mammals	Spines;	E	-20%	Seed	N	P	N	[43]
		Effectiveness of pollinators	E	22% less time per flower	Pollinator foraging time				
<i>Senecio jacobaea</i> (Asteraceae)	Natural herbivore community	Pyrrrolizidine alkaloids	D	0%	Flower	N	P	N	[44]
<i>Arabidopsis thaliana</i> (Brassicaceae)	Natural herbivore community	Glucosinolates	D	$\beta = -0.27$	Fruit	N	G	Y	[45]
		Trichomes	D	$\beta = -0.46$	Fruit				[46]
		Tolerance/resistance tradeoff	E	0%	Tolerance				
<i>Ipomoea purpurea</i> (Convolvulaceae)	Generalist herbivores, simulated damage	Genetic correlation btw resistance and tolerance	E	$r = -0.943$	Seed	B	G	N	[47]
<i>Ascophyllum nodosum</i> (Fucaceae)	<i>Littorina obtusata</i>	Phlorotannin	D	25–54%	Annual growth	N	P	Y	[17]
<i>Pinus edulis</i> (Pinaceae)	<i>Matsucoccus acalyptus</i>	Tradeoff between resistance and mycorrhizal fungi colonization	E	0%	EM fungi colonization	N	P	N	[14]
<i>Plantago lanceolata</i> (Plantaginaceae)	<i>Junonia coenia</i>	Iridoid- and phenylpropanoid glycosides	D	0%	Growth	N	P	Y	[48]
<i>Psychotria horizontalis</i> (Rubiaceae)	Pyralidae, Ctenuchidae	Tannins	D	Negative partial correlation	Growth	N	P	N	[16]
		Toughness	D	0%	Growth				
<i>Datura wrightii</i> (Solanaceae)	Natural herbivore community	Glandular trichomes	D	34–73%	Seed	N	P	Y	[22]

^aBox 3 fully explains the column headings.

^bAbbreviations: B, inbred lines; C, crop population (not genetically controlled); D, direct resistance cost; E, ecological cost.; I, isogenic lines; N, natural population; R, randomized; S, recurrent selection.

^cMagnitude of cost was acquired from data in text or was estimated from graphical presentations of data. Calculation methods are described in Box 3.

^dPhenotype/Genotype.

Table 2. Studies of costs of induced resistance

Plant species	Herbivore species	Reason for cost	Cost type ^a	Magnitude of cost ^b	Fitness measure	Genetic background ^c	P/G ^d	Multiple popul.	Refs
<i>Pastinaca sativa</i> (Apiaceae)	Induced with simulated herbivory	Induced myristicin, furanocoumarins	D	8.70%	Biomass, growth	N	P	N	[49]
<i>Lepidium virginicum</i> (Brassicaceae)	<i>Myzus persicae</i> , <i>Blapstinus</i> sp.; induced with <i>Pieris rapae</i>	No competition Competition	D E	0% 39%	Biomass Root biomass	N	P	Y	[50]
<i>Raphanus raphanistrum</i> (Brassicaceae)	<i>Pieris rapae</i>	Indole glucosinolate induction	D	6%	Pollen production	R	P	N	[51]
	<i>Pieris rapae</i> , <i>Lepus</i> spp., <i>Phylotreta</i> spp.; induced with <i>P. rapae</i>	Induction increases damage by specialists	D E E	0% 66% more damage 167% more damage	Seed Oviposition by <i>P. rapae</i> Damage by beetles	N	P	N	[52]
<i>Cucumis sativus</i> (Cucurbitaceae)	<i>Tetranychus urticae</i> , <i>Diabrotica undecimpunctata</i>	Cucurbitacins; increased susceptibility to specialists	D E	0% 400%	Biomass More damage	I	G	N	[30]
<i>Gossypium thurberi</i> (Malvaceae)	<i>Bucculatrix thurberiella</i> , induced with <i>B. thurberiella</i>	Induction by herbivore	D	0%	Seed	N	P	N	[53]
<i>Triticum uniaristatum</i> (Poaceae)	<i>Rhopalosiphum padi</i> , induced with <i>R. padi</i>	Induced hydroxamic acids	D	0%	Biomass	n/a	P	N	[54]
<i>Lycopersicon esculentum</i> (Solanaceae)	Induced with MeJA	Induced polyphenol oxidase, peroxidase	D	33%	Seed	C	P	N	[55]
	Natural herbivore community; induced with MeJA	Defensive chemicals	D D	25–30% 0%	Flower Seed	C	P	N	[56]
	<i>Spodoptera exigua</i> ; induced with MeJA and BTH (SAR pathway)	Herbivore–pathogen resistance tradeoff	D E	0% 0%	Fruit Pathogen lesions	C	P	N	[57]
<i>Nicotiana attenuata</i> (Solanaceae)	Natural herbivore community, induced with MeJA	Induction of nicotine	D	26%	Seed	N	P	Y	[25]
	Induced with MeJA	Induced nicotine; ‘opportunity cost’ with competitors	D E	0 61%	Seed Fitness increase of competitor	N	P	N	[58]
<i>Nicotiana sylvestris</i> (Solanaceae)	Induced with MeJA	Nicotine	D D	12% 0%	Flower Seed	n/a	P	N	[59]
		Decreased competitive ability	E E	0% 50%	Flower Seed				

^aAbbreviations: B, inbred lines; C, crop population (not genetically controlled); D, direct resistance cost; E, ecological cost.; I, isogenic lines; MeJA, methyl jasmonate; N, natural population; R, randomized; S, recurrent selection.

^bMagnitude of cost was acquired from data in text or was estimated from graphical presentations of data. Calculation methods are described in Box 3.

^dPhenotype/Genotype.

the general conclusions drawn from this review, as well as our discussion of methodological issues, have widespread implications for many fields concerned with the costs of resistance, including both plant and animal resistance to pathogens. We conclude by posing questions that arose from our survey.

In our survey, we followed the criteria established by Bergelson and Purrington [5] closely (Box 2). In spite of our precautions, we might have missed pertinent papers, but these omissions should not be biased with respect to detecting costs. We tabulated several attributes from the studies to determine the nature of resistance and the type of costs involved (Box 3). We examined the prevalence and magnitude of costs to herbivore resistance.

Disadvantages of examining natural populations

More investigators collected seed or propagated clones from naturally occurring genotypes than from genotypes created to control for genetic background (Tables 1,2). There are several problems associated with using these field-collected plants to evaluate costs of resistance. Most importantly, measured costs might result from artifacts associated with non-random mating, such as inbreeding depression, or from costs associated with traits in linkage disequilibrium (e.g. non-random associations between alleles at physically unlinked loci).

Natural populations can exhibit significant levels of inbreeding and inbreeding depression [8,9]. Highly inbred families or populations, such as those of

Table 3. Percentages of explorations^a demonstrating costs

(a) Percentages of explorations demonstrating costs				
Genetic background	Controlled: 56% (<i>n</i> = 18)		Not controlled: 55% (<i>n</i> = 33)	
Cost type	Direct: 51% (<i>n</i> = 35)		Ecological: 62% (<i>n</i> = 16)	
Resistance type	Induced: 52% (<i>n</i> = 23)		Constitutive: 57% (<i>n</i> = 28)	
(b) Explorations demonstrating costs by investigation type (%)				
Genetic background	Direct resistance costs		Ecological costs	
	Induced	Constitutive	Induced	Constitutive
Controlled	33% (<i>n</i> = 3)	55% (<i>n</i> = 11)	100% (<i>n</i> = 1)	67% (<i>n</i> = 3)
Not controlled	42% (<i>n</i> = 12)	67% (<i>n</i> = 9)	71% (<i>n</i> = 7)	40% (<i>n</i> = 5)

^aAn exploration is a single test for cost within a study. Seed and flower production measured in the same study were considered separate explorations, because seed production is a better estimate of female fitness and flower production of male fitness.

extensively selfing species, for example *Arabidopsis thaliana*, might have other genes associated with resistance traits that could be responsible for costs [4]. Resistant and susceptible inbred lines could be expected to have many differences, and the attribution of costs solely to a difference in resistance traits would be misguided. Resistance can also result more from inbreeding depression than, for example, from the particular level of a secondary compound. Confounding inbreeding depression with a 'resistance trait' would be especially problematic for studies in which no mechanism of resistance is specified (i.e. when resistance is only assayed through insect choice or damage levels). In these cases, it is difficult to know whether lack of attack is caused by lack of plant vigor (e.g. plant vigor hypothesis [10]), by inbreeding depression [11] or by 'resistance' traits. With concomitant measurements of the putative resistance trait, this concern can be partially addressed. Of interest would be more studies examining the relationship between heterozygosity and resistance [12], and between inbreeding and resistance [11].

Even obligately outcrossing species might not mate at random and thus might also suffer artifacts of linkage disequilibrium. Neighbors are often closely related, and there can be fine-scale genetic structure

within plant populations [13,14]. In addition, damage or resistance might determine flowering phenology and subsequent mating partners. Assortative mating among resistance types could occur if susceptible plants receive more damage and flower later [15] than do resistant plants. Alternatively, if resistant plants grow more slowly [2,16,17] and flower later than do susceptible plants, then associations generated by assortative mating and caused by a growth/defense tradeoff could obscure the detection of costs.

Finally, studies that do not control for genetic background might only measure phenotypic correlations between resistance traits and fitness. Phenotypic correlations are often misleading with respect to the underlying genetic correlations among traits [18]. Genetic correlations between resistance and fitness best determine whether costs can constrain the evolution of plant resistance.

Remedies for unknown genetic backgrounds

Creating seed from random matings within a natural population can disrupt associations not maintained by selection and can reduce the problems of linkage disequilibrium [4,5]. If selection does favor strong linkages between resistance and other traits, then these linkages represent legitimate sources of (at least current) costs of resistance in natural populations. For example, selection for increased levels of iridoid glycosides also resulted in taller *Plantago lanceolata* plants [19], which might be more susceptible to browsing [19,20]. This association of traits was still evident after four generations of selection on iridoid glycosides [19] and could potentially be a cost of resistance owing to a linked trait.

Another way of using genotypes from natural populations would be to sample multiple natural populations. It is unlikely that spurious linkages with resistance traits would result in the same pattern of resistance costs across multiple, natural populations. Just seven of the studies reviewed examined multiple populations. Such studies are extremely valuable, in that the expression of costs is often environmentally determined [21,22], and documenting the prevalence of costs across numerous natural settings is essential to understanding whether costs constrain the evolution of resistance.

Induced resistance and genetic background

Studies of induced resistance might be more robust to problems associated with a lack of control for genetic background. By randomizing the application of elicitor treatments [typically, plant signaling hormones such as methyl jasmonate (Me JA), or herbivores] to induce plants, experimenters can effectively randomize genetic background and genetic heterogeneity among induction treatments. The disadvantage of experimental manipulations of induced resistance is that elicitors might have pleiotropic effects that can alter plant metabolism, and other traits not essential to the expression of resistance. Studies using

Box 2. Selection criteria for studies reviewed

- We searched the following journals: *Agricultural Systems**, *Agronomy Journal**, *American Journal of Botany**, *Annals of Botany**, *Annual Review of Ecology and Systematics**, *Crop Science**, *Ecology**, *Euphytica**, *Evolution*, *Journal of Applied Ecology**, *Journal of Ecology**, *Journal of Experimental Botany**, *Plant Science Letters**, *The New Phytologist**, *Oecologia*, *Oikos*, *Vegetatio**. [*Bergelson and Purrington (1996) journals]
- We also conducted a key word search in BIOSIS using 'cost#' and 'resistan#'' and 'cost#' and 'defens#'
- Dates searched: 1994–present
- For studies of constitutive resistance, the study must have identified the genetic background of the plant species investigated
- We excluded cultivars unless they were isogenic or near-isogenic lines
- We excluded transgenic crops unless the appropriate transformation controls were included
- Studies were required to examine fitness (or a close measure) in both the presence and absence of herbivores, unless costs of the putative resistance trait were detected in the presence of herbivores

Box 3. Attributes recorded from literature survey

- Identity of plant species
- Identity of herbivore species
- Putative resistance trait (present or previous study should have shown that the trait, or increasing amounts of the trait, conferred resistance to herbivores.)
- Type of cost [direct resistance cost (D) or ecological cost (E)] When only fitness traits (seed set, etc.) were measured, costs were categorized as direct (see 'Ecological costs' section for discussion)
- Magnitude of cost (from data in text or estimated from graphical presentations of data). Zero values represent both 0% reduction in fitness and values not significantly different from 0
- For studies comparing resistant plants with susceptible plants: Magnitude = $\{[1 - (\text{fitness of resistant type}/\text{fitness of susceptible type})] * 100\}$
- For studies describing the relationship between resistance level and fitness: Magnitude = slope of regression of fitness on resistance
- For studies examining ecological costs: Magnitude = $\{[1 - (\text{ecological trait for resistant type}/\text{ecological trait for susceptible type})] * 100\}$ (e.g. 66% more damage by other herbivore species)
- Fitness estimate measured (used the measure that most closely reflected fitness)
- Type of genetic background (B, inbred lines; C, crop population, I, isogenic or near-isogenic lines; N, natural population; R, randomized by random mating; S, recurrent selection for resistant and susceptible lines)
- Phenotypic resistance (P) (only resistance phenotype is known) or genotypic resistance (G) (resistant plants are known to genetically differ from susceptible plants)
- Multiple populations examined in study (Y, yes; N, no).

non-herbivore elicitors (such as Me JA) differ greatly in how closely the treatment mimics real herbivore-caused elicitation, and thus the accuracy of such treatments becomes an important consideration in the evidence for costs [23]. Given this disadvantage, studies that use herbivores to elicit the induced response in plants via small amounts of damage might be preferable, although leaf-area loss caused by damage must also be factored into plant response. Although the non-target effects of elicitors are potentially problematic, the specificity of the cues required for the expression of induced resistance traits might preclude some of these concerns.

Transgenic plants

The use of genetic transformation technology provides a novel approach to manipulating plant resistance traits. Novel resistance traits, such as the bacterially derived herbivore toxin *Bt*, can be inserted into plant genomes. In addition, endogenous genes can be silenced, or 'knocked out' to measure costs of production of particular gene products. Although this powerful technology might provide solutions to many problems, the use of transgenic plants to the study of costs of resistance requires appropriate controls. The insertion of novel genes necessitates controls for positional effects (where the gene is inserted), vector controls (which vector is used to insert the gene) and selection for a single copy of the transgene (in many cases multiple copies can be inserted into the same locus in tandem). Other concerns with transgenic methodology are the mutagenic effects of insertion, and variation in the levels and development pattern of gene expression (I. Baldwin, J. Bowman and C. Langley, pers. commun.). Multiple, independently transformed lines will provide a better estimate of the cost of resistance in

any transgenic study, as the results will not reflect specific interactions between the transformation (e.g. insertion or silencing) and a single genetic background. These techniques will become more useful in the future, as controls become easier to achieve. In our survey, however, we found no studies using transgenic plants that undertook these extensive controls.

Results from our survey: Prevalence of costs

Overall, costs were detected in 76% of the studies examined and in 82% of the studies in which genetic background was controlled. This latter result is consistent with Bergelson and Purrington's study [5], which showed that controlling genetic background increased the likelihood of detecting costs. In our survey, however, the percentage of studies detecting costs (76%) was substantially greater than the 33% of studies examined by Bergelson and Purrington.

It should be noted that the taxa examined in genetically controlled studies were heavily biased towards the Brassicaceae (five out of ten studies, two species), with an additional two species in Solanaceae, and one each in Curcubitaceae, Convolvulaceae and Plantaginaceae. We included multiple studies of the same species if they examined different traits or costs (as in Bergelson and Purrington [5]). This phylogenetic bias means that these studies are not truly independent tests of the presence of costs. Studies that factor out the importance of phylogeny could help correct this potential bias.

Studies that did not control genetic backgrounds detected costs only 73% of the time. Although the diversity of plant families was greater in this collection of studies, the distribution of studies still was not very equitable among families [Solanaceae (four species), Brassicaceae (three species), Asteraceae (two species), Apiaceae, Fucaceae, Pinaceae, Plantaginaceae, Poaceae, Rubiaceae (one species each)].

Multiple explorations of costs

In Bergelson and Purrington's review [5], a study was counted as showing a cost if any one investigation within that study documented a cost. Because many of our studies undertook multiple explorations of costs (e.g. examination of both ecological and direct resistance costs in the same paper), we have further tabulated results of the separate explorations for different types of cost and resistance (Table 3). The rate of detection of costs was generally lower for any single exploration than on a study-wide basis. Table 3 shows that the difference in detection rates between our study and that of Bergelson and Purrington [5] does not hinge on the inclusion of ecological costs in our survey. Finally, it is clear from Table 3 that few studies investigating the costs of induced resistance and ecological costs also rigorously controlled for genetic background.

Magnitude of costs

The magnitude of direct resistance costs, when present, was quite large, ranging from 6% to 45% in

controlled background studies, and from 8.7% to 73% in studies of natural populations. Given that $[(1 - (\text{cost}/100))]$ is the relative fitness of the resistant genotype in the absence of the selective agent, these figures represent a strong selective disadvantage to resistance in herbivore-free environments. These magnitudes are generally greater than those reported by Bergelson and Purrington [5]. Lest we feel these values extreme, however, it should be noted that, in two studies demonstrating large costs of resistance, the BENEFITS OF RESISTANCE in the presence of herbivores exactly outweighed the costs [24,25].

Ecological costs of resistance

Since the review by Bergelson and Purrington [5], more studies have explored the possibility that costs might be expressed in the context of interactions with other species; ~40% of our studies investigated ecological costs of resistance. These studies represented four of the basic types of ecological cost (Box 1). There is a dizzying array of potential ecological costs of resistance, and few of these costs of resistance have been investigated empirically [26].

Tradeoffs among traits conferring resistance against different plant enemies could constrain the evolution of resistance. For example, silencing the *PAL2* transgene in tobacco, *Nicotiana tabacum*, increased resistance to *Heliothis virescens* larvae, but suppressed systemic acquired resistance (SAR) against pathogen attack [27]. This result suggests that resistance pathways against different enemies might compete for shared biochemical precursors and thus might not be fully deployed simultaneously; however, in *A. thaliana*, there was no evidence for cross-talk between these pathways [28]. The degree to which these pathways constrain each other's action is still unclear.

There is also evidence that the same gene can have multiple ecological functions that pose conflicting problems for plants. For example, plant traits that deter one herbivore can be attractive to others, particularly specialists [29,30]. Other costs might occur at the expense of attracting mutualists. Volatiles released when plants are damaged not only attract predators and parasites, but also attract

herbivores [31]. Additionally, resistant plants that have higher concentrations of secondary compounds in fruits, floral tissues or nectar (e.g. toxic nectar [32]) than do susceptible plants, might be less attractive to pollinator or disperser mutualists.

Of all the studies addressing ecological costs, only 46% examined the costs in terms of reduced plant fitness; many studies only measured the consequences of resistance traits on other organisms (e.g. decreased pollinator attraction). Measuring the fitness consequences of changes in these interactions is the crucial next step toward understanding the importance of indirect costs.

Finally, when tests for costs of resistance are done in the field, ecological costs might be important, but misguidedly ascribed to direct costs. For example, if resistant plants are more pollinator-limited than are susceptible plants, then these ecological costs will be undetected, if fruit set is the sole measure of cost. In this case, reduced fruit set would generally be interpreted as an allocation cost. Thus, in field trials where interactions with other community members are prevalent, hidden, indirect costs might be part or all of reported direct costs.

Conclusions

We found 33 studies published during the last six years that examined ecological and direct resistance costs of constitutive and induced defenses against herbivores. There was high prevalence of direct resistance costs (53%) as well as indirect, ecological costs (59%), and the detection of costs was similar both for constitutive (57%) as well as induced resistance (52%). Costs were more likely to be detected when genetic background was controlled; thus, we suggest that more studies employ controlled designs. Finally, many studies of ecological costs have not measured these costs in the currency of plant fitness. More work is needed to determine the relative importance of direct costs versus indirect costs of plant resistance.

Many exciting challenges still remain for researchers investigating the costs of induced and constitutive resistance to herbivory. Particularly intriguing questions include:

Are there costs associated with resistance to herbivory in genetically modified (GM) crops?

Many GM crops have genes inserted that confer resistance to herbivores (such as the *Bt* gene), and these crops can produce higher yield than can non-GM crops in the presence of herbivores [33]. But, in years when herbivores are rare, it is relatively unknown whether there is decreased yield in these resistant GM crops. Few published tests addressing this question have used the appropriate controls for genetic background.

Do direct resistance costs affect male and female function equally in hermaphroditic plants?

Many studies have provided convincing evidence that there are costs associated with resistance measured in

Glossary

Allocation cost: a resource-based tradeoff between fitness and resistance.

Benefits of resistance: when the fitness of resistant plants is greater than that of less resistant plants in the presence of enemies.

Constitutive resistance: resistance that is always expressed in the plant (independent of damage).

Costs of resistance: when the fitness of more resistant plants is lower than the fitness of less resistant plants in the absence of enemies.

Direct resistance cost: a tradeoff between fitness and resistance that is not mediated by interactions with other species (e.g. allocation costs, auto-toxicity, opportunity costs, changes in phenology, growth rate, dormancy and other auto-ecological traits, and increased susceptibility to abiotic stresses).

Indirect resistance costs (ecological costs): tradeoffs between fitness and resistance mediated by interactions with other organisms.

Induced resistance: resistance that is expressed only after a plant is damaged.

Resistance: a plant trait that reduces damage by herbivores.

fruit or seed production; however, whether there are costs of resistance in terms of seeds sired remains unmeasured. Costs associated with siring success might reflect direct resistance costs with respect to pollen, as well as ecological costs of deterring mutualistic pollinators, especially for self-incompatible plants.

What are the prevalence and magnitude of ecological costs of resistance?

There is no debate that ecological costs of resistance, such as increased parasite loads or decreased tolerance, exist. However, only a few of the many types of ecological cost have been investigated experimentally. Even fewer studies have examined multiple ecological costs within the same system. How resistance alters interactions with co-occurring organisms, as well as how those altered interactions influence plant performance and, ultimately, plant population dynamics, deserve more attention.

Are there costs associated with third-party resistance?

Many plants are defended indirectly via the actions of other species. Extrafloral nectar, food bodies and domatia (plant structures, such as hair tufts, that give shelter to predators) are all resources provided by plants to attract enemies of herbivores. To date, few studies have investigated the costs of these resources in both the presence and absence of herbivores. We think that these indirect defensive traits are important to explore in future studies on the ecological costs of resistance.

Understanding the prevalence and magnitude of costs of resistance is central to understanding selection pressures on plant defense. Our update demonstrates that many studies have documented costs of resistance in recent years. We hope this review motivates further studies on the ecological and direct resistance costs of herbivory in natural and agricultural ecosystems.

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Adaptive population divergence: markers, QTL and traits

John K. McKay and Robert G. Latta

Molecular markers appear to be poor indicators of heritable variation in adaptive traits. Direct comparison of population structure in markers with that in traits is made possible by the measure Q_{st} , which partitions quantitative genetic variation in a manner analogous to F_{st} for single gene markers. A survey of the literature reveals that mean Q_{st} is typically larger than and poorly correlated with mean F_{st} across 29 species. Within species, Q_{st} varies widely among traits; traits experiencing the strongest local selection pressures are expected to be the most divergent from molecular F_{st} . Thus, Q_{st} will be particularly relevant to conservation efforts where preserving extant adaptation to local environments is an important goal. Recent theoretical and simulation studies suggest however that F_{st} is a better predictor of the pattern of allelic differentiation at quantitative trait loci (QTLs) than is Q_{st} in random mating populations, in which case allelic variation at QTLs might be better assessed by molecular markers than will extant variation in the traits themselves.

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'A major unresolved issue is the relationship between molecular measures of genetic diversity and quantitative genetic variation' (Frankham [1])

Molecular genetic markers have played a major role in evolutionary biology. As molecular methods have become cheaper, faster and involve less invasive sampling, they have become increasingly popular in conservation [2,3], where there is often a clear need for rapid decision making. For example, because genetic differences among populations are often considered

worthy of conserving [2–5], many studies apply a criterion, assigning conservation priority to populations (or clades of populations) that are reciprocally monophyletic, because these probably represent independently evolving clades or evolutionarily significant units (ESUs) [5]. There are several definitions of ESU in the literature, which vary in the degree of emphasis placed on molecular versus ecological criteria [2–6]. Such definitions have crucial importance in the light of conservation legislation, where boundaries of ESUs must be drawn before legal protection status can be assigned [2–4]. However, locally adaptive genetic diversity within units is likely to be of greater importance when choosing populations that are most suitable as translocation or restoration sources. In this case, adaptive genetic differences among populations can lead to outbreeding depression if divergent populations are mixed [7].

Several reviews have identified testing the assumption of an association between marker diversity and adaptive diversity as a pressing research concern [1,8–10], and warn against the gradual replacement of ecological data with molecular criteria when diagnosing units of conservation [2,3,10]. Two recent studies use a formal meta-analysis to test the relationship between molecular and quantitative variation, both within [10] and among populations [11]. Here, we focus on measures of divergence or population structure [11], because these are most relevant to the